Annals of Botany

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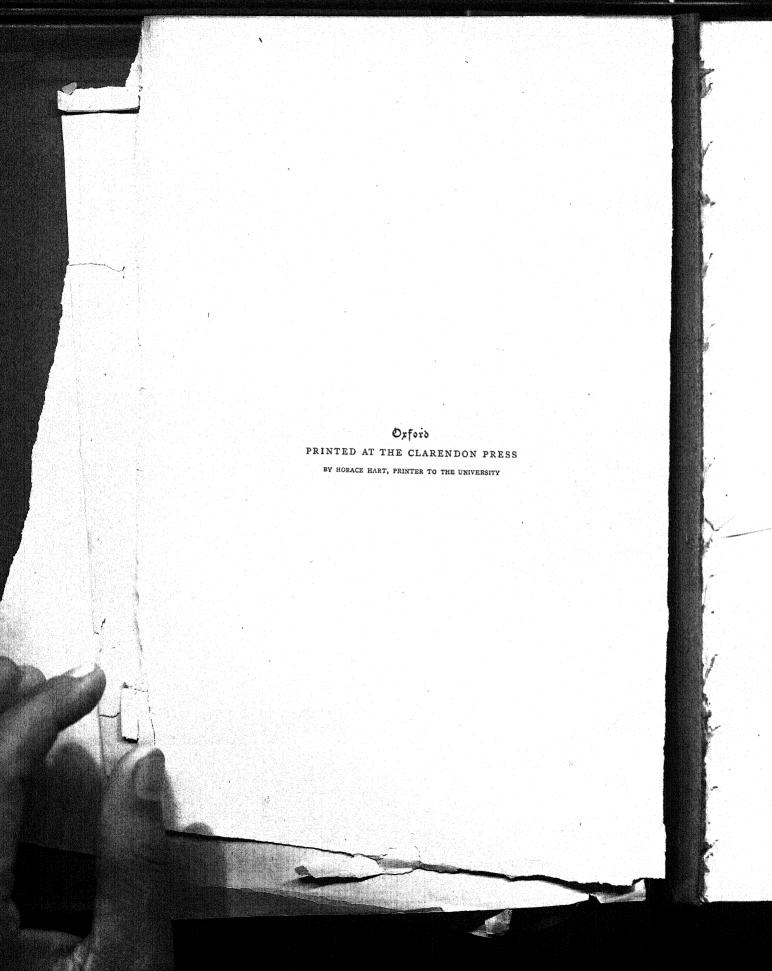
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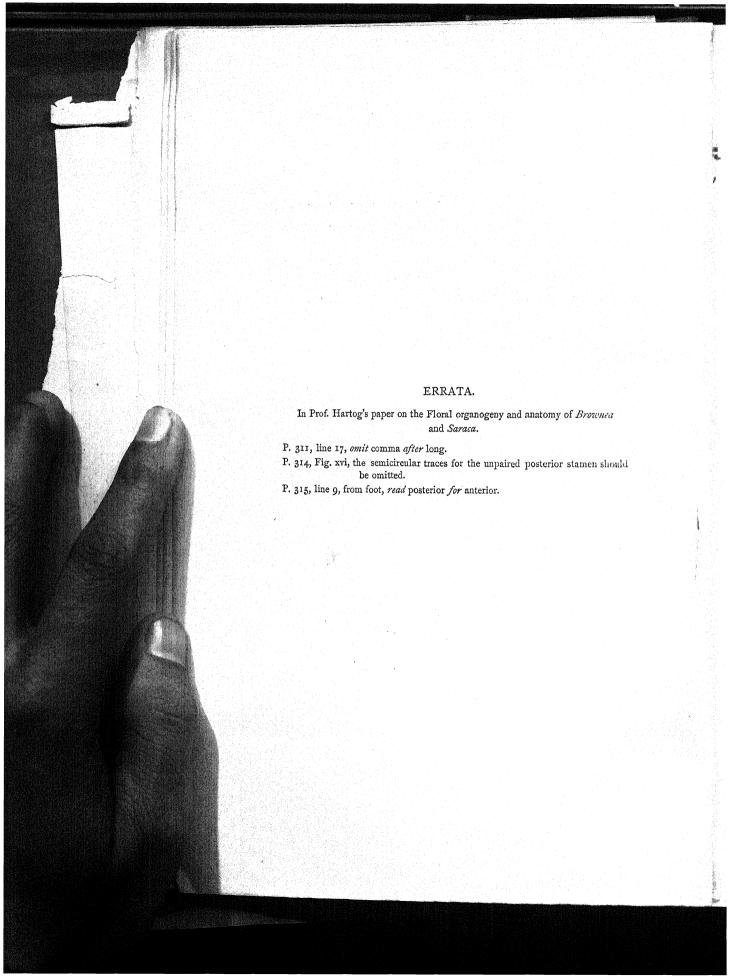
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Notes on the Plasmodium of Badhamia utricularis and Brefeldia maxima.

BY ARTHUR LISTER.

With Plates I and II.

THE study of the plasmodium of Mycetozoa has received considerable attention on the Continent, and the account of the life-history of these remarkable organisms given by De Bary in the last edition of his 'Comparative Morphology and Biology of Fungi, Mycetozoa and Bacteria,' as well as those by Zopf and Sachs, afford an interesting view of their habits and properties; but the investigations recorded by these authorities appear to have been chiefly directed to Fuligo varians and various species of Physarum, and in following the development from spore to sporangium of Chondrioderma difforme.

Although the plasmodia of many Mycetozoa may be induced to crawl on a glass plate, where their rhythmic streaming may be observed, yet the comparatively short time that elapses between their emerging from hidden recesses in the substance of rotten wood, and their changing into sporangia, renders the greater number of them unsuitable for prolonged examination; none that I have met with is so favourable in this respect as that of *Badhamia utricularis*, which wanders for the most part over the surface of dead stumps, and can easily be cultivated in glass boxes or under bell-jars. Another advantage in dealing with the plasmodium of *Badhamia* is the facility with which it can be thrown into

a sclerotium or resting stage. In this condition it may be stored away and can be brought back again into the active state by the application of water, at any time within several months. I shall have occasion to revert to this later.

The notes I now offer refer principally to this species, which I have kept in constant streaming movement on various

kinds of woody fungi for more than a year.

In January, 1877, Badhamia was abundant in my garden at Leytonstone on some old hornbeam logs, which were also overgrown with extensive patches of Corticium puteanum, an effused fungus consisting of a central portion, brown and lurid from the multitude of its spores, surrounded with a white byssoid margin. The Badhamia advanced over the Corticium, entirely consuming the hyphae, or cut broad paths through the larger patches, leaving the bark to all appearance clean and bare where the plasmodium had passed on.

I allowed the plasmodium which had been thus feeding, to crawl on a glass plate, when its usual colour of rich chrome-yellow had changed to deep brown; this alteration of colour was shown by the microscope to be caused by the countless undigested brown spores of the *Corticium* held in suspension. These spores could be seen hurried along in the torrents that coursed through the branching channels, rolling over and over among the minute yellow granules and transparent vacuoles of the plasmodium.

When this had retreated from the glass plate, a map of its lace-like network was left behind, formed by the ejection on each side of the veins, of thousands of the *Corticium*-spores mixed with other refuse matter.

I placed some wet cotton-wool in front of the still dingy plasmodium; this it readily penetrated, and afterwards emerged possessing its normal yellow colour, leaving the wool charged with spores and other *débris*; it soon after changed to sporangia which became black in the course of about thirty-six hours, and as they dried assumed the blue-grey colour characteristic of the species.

The consumption of the *Corticium* was so interesting a fact that I exhibited specimens of the hornbeam bark with the *Corticium* in the act of being invaded by the plasmodium at a meeting of the Linnean Society. I also showed under the microscope the streaming plasmodium on a glass plate.

The difficulty of obtaining satisfactory observations when the plasmodium is spread over an exposed surface led me to cultivate it in glass boxes suitable for examination on the stage of the microscope (Fig. 5). The boxes are easily made, with two sides of thin glass measuring three by two inches fitted with wood ends half an inch wide, and a glass bottom, the whole fastened together with stiff glue and varnished at the points of junction and over the wood with canada balsam; a glass slip half an inch wide serves as a cover secured with an elastic band; in such boxes the plasmodium can be kept for any length of time in a damp atmosphere.

Besides the Corticium before mentioned, most effused fungi as well as thin species of Dacdalea and Polyporus, especially P. versicolor and P. adustus, afford good nourishment to the plasmodium of *Badhamia*, though in cultivation these are apt to grow Mucor which leads to the decay of the plasmodium if allowed to spread; but its favourite food is Stereum hirsutum, a fungus that abounds on logs of oak and hornbeam, and on which Badhamia is constantly found during the winter months. With this we have no trouble from Mucor, while it is so rich a pabulum that in April and May of last year I cultivated plasmodia thickly covering an area of at least thirty inches, all of which had grown from a small quantity creeping over a piece of Stereum about the size of a half-crown with which I commenced operations on April 6; and in addition to this plasmodium which remained in a creeping state, an equal amount had changed into sporangia in glass boxes or under bell-jars.

Although the plasmodium grew very rapidly during the summer, and showed such vigour that it frequently spread completely over the glass shades placed over the piles of Stereum if I omitted for two or three days to supply fresh food, yet none changed to sporangia between May 24 and September 27.

In hot weather, considerable attention is needed to keep the plasmodium in health, a fresh supply of Stereum must be frequently added, and the decayed bits cleared away. The new pieces are usually crawled over in the course of a few hours, and can be taken off and placed in a glass box for observation, or put under a glass shade with more Stereum to start a fresh colony. In the colder months no serious consequences follow if a pile is left alone for a week, the plasmodium may settle down with sluggish movement or pass into a resting stage; but in the height of summer a promising-looking colony will often fall into foul decay in twenty-four hours if it is neglected.

When plasmodium is placed in a glass box it will soon crawl up the sides, and it is then in a favourable condition for observation (see Fig. 1). The following experiments bearing on its manner of feeding have been conducted with these moist chambers.

In the first place I submit the results of a number of observations with regard to the action of the plasmodium of *Badhamia* upon starch, which has been stated on the authority of Dr. Wortmann to have been absorbed by the plasmodium of *Fuligo*¹.

In arranging for these experiments, I cut slices of raw potato and pounded them in a mortar; I then carefully washed the pulp so as to collect only the unbroken starchgrains, as an appearance of erosion is easily given by a slight bruise. Starch obtained from this source seems to be better for our purpose than any other, on account of the large size and regular form of the grains.

If this raw starch is spread with water on the side of a glass box in front of an advancing wave of the plasmodium, it is simply incorporated without any material stimulus to

¹ See De Bary, Morphology and Biology of the Fungi, Mycetozoa and Bacteria. Engl. ed. p. 452.

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Badhamia utricularis and Brefeldia maxima.

the flow being set up, and as a rule no change whatever takes place in the starch-grains; they are seen to be swept over by the streaming currents, or carried along the larger veins, and after five or six days' retention, they may be cast out or left behind on the glass with no more visible alteration than if they had been grains of sand.

On one occasion I watched what I supposed at the time to be the actual absorption of starch. On May 26, 1887, I was observing plasmodium in a glass box on the side of which I had spread raw starch scraped from potato. noticed a body having the size and general form of a starchgranule, with a slight indentation, and drew it with camera lucida (Fig. 16 a); a thin stream of plasmodium was then flowing over it. I left the glass box on the stage of the microscope, with the drawing below the camera; after an hour's interval I looked again and found that the object had diminished to the size b in Fig. 16; from that time it was under constant observation for an hour and a half, during which it passed through the forms c, d, e, f, g, drawn with the camera at intervals of about a quarter of an hour; the last fragment then disappeared in the film of plasmodium which had continued to stream with the regular rhythmic alternate flow during the whole of the time. From subsequent experience I can hardly suppose this to have been a grain of raw starch, for I have since watched hundreds of these grains, often for hours without intermission, and in no single instance have I been satisfied that any change has taken place, nor have I seen any appearance of erosion of raw grains left by retreated plasmodium that could not be explained by the effect of bruising.

I have frequently examined raw starch which has remained for a week and from that to ten days constantly enveloped in moving plasmodium, and not a grain has shown the slightest erosion; yet I give the above observation as possessing considerable interest as an undoubted instance of the absorption of a solid substance.

If instead of using starch in its raw state, it is first warmed

with water in a test-tube, just sufficiently to swell most of the grains, the effect is very different from what I have described. On the plasmodium reaching this swollen starch, it rapidly advances in a concentrated opaque mass, and at the same time the flow along the more distant veins is much accelerated. After some hours, when the wave of plasmodium has retired, all the completely swollen grains are found to have disappeared, while those that have been only slightly affected by the warm water have lost their softer portions and show their margins more or less eroded according to the length of time they have been subjected to the action of the plasmodium. In cases where repeated waves have passed over the starch, the erosion of such imperfectly softened grains is markedly greater, but they are not entirely consumed, and there always remains a large residuum of whole or eroded grains. Application of iodine shows the side of the box to be strewn with small fragments of starch.

It is very difficult to observe the process of absorption, because the stimulus given to the plasmodium occasions it to accumulate in a broad border, often 1 mm. in thickness, and it is only after its retreat that we can see the change that has taken place.

The plasmodium with which one of these observations was made, had crawled upon a glass shade from a pile of Stereum over which it had been placed. I took off the shade and half filled it with water, and with a feather gently detached the film of plasmodium, allowing it to float about; I then passed under it a piece of wet cotton wool, and in this way was able to collect it upon the wool without materially disturbing the network of veins. I placed it in a clean glass box, and with a pair of forceps took out the remaining floating pieces and added them to the rest; by these means the streaming of the plasmodium is hardly checked, and it will often begin to climb up the side of the box in the course of a few minutes. This method is useful when it is desired to make experiments with pure plasmodium free from any foreign matter.

I now proceed to relate observations on the absorption of various fungi.

On October 10, 1887, I placed a thin section of the pileus and gills of Agaricus campestris, measuring 7 × 4 mm., in front of an advancing wave of plasmodium, which at once concentrated in a turgid mass upon the agaric, and in the course of an hour had entirely enveloped it. On the retreat of the plasmodium after some hours, not a trace of the mushroom remained. I have repeated this again and again with always the same result; a sluggish condition of the plasmodium is invariably revived and rapid streaming in the surrounding veins towards the object is set up when this agaric is offered to it.

Several experiments were made with slices of the pileus of *Boletus flavus*, which were even more greedily devoured than the mushroom.

On October 11, I placed a section of the pileus and gills of Agaricus melleus before a wave of plasmodium. The action was less rapid than in the other cases, but in two hours the section was densely enveloped, and next morning, when the plasmodium had withdrawn, nothing remained on the glass but a heavy grey deposit of granular and slimy dibris.

As the tissue of the pilei of the fungi hitherto used is composed of delicate hyphae, I next tried an experiment with harder material. On October 12, I cut a section of the stem of Agaricus melleus from a specimen which was tough and mature, the buff-coloured outer coat being especially firm, and the hyphae strong. I placed the section in front of a thin film of plasmodium (Fig. 1). Almost immediately on its touching the first threads of the agaric a concentration took place as in former instances. Figs. 2, 3, 4 show the manner in which the turgid border advanced. In less than two hours the whole piece was overspread, but in this case the absorption was not so rapid as it was with the softer tissue, and the section could be seen beneath the plasmodium for several hours. On the following morning the plasmodium had with-

drawn on to the Stereum in the box, and all that remained of the section on the glass side was a slimy deposit in which were scattered a few broken hyphae which I concluded had belonged to the tough outer bark.

On October 3, I experimented with a section of the gills and pileus of Agaricus rubescens. On the plasmodium reaching the section, the hyaloplasm became in some way affected, and appeared to absorb water, for it rapidly penetrated among the hyphae unaccompanied by granules and stained the section throughout gamboge-yellow. This influence on the hyaloplasm seemed to destroy its protecting power, and at the point of contact the granular plasmodium gushed out from the interior in the form of multitudes of globular bodies measuring 15μ to 25μ in diameter, each enclosed by a thin covering of hyaloplasm. Some of these floated into the surrounding water showing amoeboid movements, and were afterwards reabsorbed into the general mass, but many lost their vitality and fell to pieces, mixing with the grey slime of dead plasmodium. It was a considerable time before the main wave of plasmodium had covered the section, which could be detected lying beneath it for some hours without much apparent change; next morning, however, on the plasmodium having retreated, only a denser mucilage remained covering the spot where the section had been placed.

This experiment was repeated with another section from the same specimen of A. rubescens; this was also stained yellow, but no breaking up of the plasmodium followed. I have, however, seen the same clusters of balls when a large supply of swollen starch was submitted to plasmodium.

Some days after I again tried with A. rubescens, but not the same specimen. The section was considerably thicker than in the former case, and, as before, the progress of consumption was slow; here, however, there was no yellow staining and no breaking up of the plasmodium, but it was not altogether a favourable diet, for on the following morning a heavy deposit of dead plasmodium was left upon the glass.

in which could be seen grey lines of undigested spores showing the remains of the gills; the hyphae had all disappeared.

On October 26, I treated plasmodium in two glass boxes with sections of the pileus and gills of Agaricus fascicularis. The action was very different from what had been observed with the other agarics and with Boletus. In one box, after the slice had remained touching the plasmodium for 3½ hours, no advance had been made; so in order to stimulate its movement, I applied a small section of Boletus flavus to the same wave and about an eighth of an inch from the A. fascicularis: in forty minutes not only was the Boletus absorbed, but the plasmodium had surged in a broad fan over the A. fascicularis which could be seen unchanged beneath it. On the following morning the plasmodium had retreated leaving the section with no apparent alteration surrounded by a mass of mucus, and here this experiment came to an end.

In the other box with A. fascicularis, at 11.50 A.M. a section of pileus and ten gills was placed in contact with a strong wave of plasmodium; at 1.10 P.M. there was scarcely any advance upon it; at 3.40 I made a note, 'fascicularis rejected.' Towards evening, however, the plasmodium advanced and enveloped the section; next morning it was left stranded and little changed. In the afternoon it was again swept over by the plasmodium, which began to prey upon the hyphae of the pileus, but it was evidently an unwholesome morsel, for it was surrounded with much grey mucus; amongst this were many isolated patches of plasmodium pushing their way in the slime with constant change of form; some appeared to have broken up into clusters of globules similar in size to the balls which escaped from the plasmodium in the experiment with A. rubescens; a few of these coalesced and were taken in by the larger patches, but the greater number fell to pieces and died. Again the plasmodium withdrew, and although the section had been subjected to its action for 22 hours, the gills had been so little affected that in the forks the spores could be seen arranged on their basidia in groups of four surrounded only by water. Now, however, another wave of plasmodium advanced over it, and when again left bare on the following morning, the third day of the contest, the section was broken into small pieces and so reduced, that not a tenth of the original quantity remained. The struggle had been a tough one, for the whole lower side of the box was covered with broad bands and patches of grey slime, through which a tangle of long strings of bright orange plasmodium was twisted in strange disorder.

To restore its healthy condition, I placed in the box a piece of fresh *Stereum*, upon which the plasmodium soon concentrated itself in rich orange turgid waves, entirely withdrawing from the old pieces which were loaded with dead refuse. The following day, October 29, I cleaned out the glass box, replacing the healthy plasmodium, and added more fresh *Stereum*, on which, after rapidly increasing in volume, the plasmodium changed into sporangia on November 17.

A species of *Merulius* with small brown spores and with a white mucedinous border, somewhat resembling *Corticium puteanum*, was quickly dissolved; here again the dense accumulation of the plasmodium prevented the process being observed.

My next experiment was with the shaggy hairs scraped from the upper surface of Stereum hirsutum, well teased apart with needles. I placed the preparation in a glass box with pure plasmodium on cotton wool. It was at once seized upon and the plasmodium spread over a space measuring an inch and a half in circumference in the course of a couple of hours; in another hour it had nearly withdrawn, leaving the bundles of hyphae apparently little changed, but close examination showed many threads to be thinned away and broken in their continuity. After four days, when waves of plasmodium had repeatedly passed over the preparation, it had diminished to about half its original amount, and a magnifying power of 560 showed fragments in all stages of dissolution. At the same time much remained in which no alteration could be observed. Other experiments gave

the same results, showing that the consumption of coarse fibres, though it does take place, is very slow.

The effect of *Stereum* on the plasmodium is very different from that produced when it feeds upon agarics; there is comparatively little residue of slimy matter, and the flow is easy and free. With agarics, on the other hand, a heavy grey mucous deposit is left upon the glass, and the veins of the retreating plasmodium are rugged and loaded with particles, the streaming being confined to a narrow central channel. This condition, however, is frequently observed under other circumstances when the plasmodium becomes sluggish. Scrapings from the hymenial surface of *Stereum* are much more rapidly dissolved than the shaggy fibres; twelve hours immersion will often be sufficient to cause the whole to disappear with the exception of the coarse hyphae.

The most remarkable activity of plasmodium that I ever witnessed was caused by the supply of this pabulum.

Plasmodium crawling over pieces of Stereum had been kept for several days in a glass box, and at the time of my observation it had spread over both sides of the chamber and was slowly retreating in a widely-meshed network of narrow veins upon the clean glass. To a point on the upper edge of the network I applied a thin pulp, about the consistence of cream, of the scraped hymenial surface mixed with water. There was at first, as I have not unfrequently seen, a shrinking backwards of the margin of the network, as if notice of the presence of a food-supply had been sent off to the more distant parts; then came on a quick stream, and in a quarter of an hour the whole side was pouring up its plasmodium with astonishing rapidity. The wide meshwork was not sufficient to conduct the abundant supply, and fresh veins started off in all directions, cutting up the broad meshes; at one time the current along them all was so precipitate that I endeavoured in vain to follow the course of the particles; they rushed across the field of the microscope at a speed that was truly amazing. While the streaming was at its full height, I noticed a brown lump about the size of a large

starch-grain, and which I took to be a piece of dead sclerotium, rush along a swollen vein until it reached a fork, when it blocked the passage. Fresh streams immediately broke out on each side of the obstruction, but the main current still forced its way along the old channel, and in so doing it cut away the dark substance as a projecting point of sand is swept off by a runnel on a sandy shore. The granular constituents streamed away along one side of the vein and were dispersed in the torrent before it had passed out of the field, and all was dissolved before the reverse flow of the current set in. Meanwhile the new veins were crossing and re-crossing the wide network in every direction, and in a few minutes it was converted into a film of rapidly-moving plasmodium perforated with small openings, ending in an opaque mass which overspread the Stereum-pulp. The stimulus soon extended all over the glass box, and in the course of a few hours the opposite side as well as some of the pieces of pileus at the bottom were overrun with rich waves.

It was a sight not soon to be forgotten; the marvellous exhibition of such active life in so low an organism was most impressive.

In my experience with the plasmodium of Badhamia the flow is usually more rapid in the larger than in the smaller veins, which is what one would expect on mere hydraulic principles. The flow through the veins continues for about a minute and a half to two minutes in one direction, when it comes to a stand and immediately reverses its course; it gradually increases in rapidity for about half a minute and retains the maximum of speed for a varying length of time, when the rate again gradually diminishes. The continuance of the flow is longer when in the direction in which the plasmodium is moving; sometimes when the advance is rapid it will go on for three minutes before the return current sets in. When a wave is spreading over the glass in ordinary conditions, the maximum flow through the veins is at the rate

of about half an inch in a minute; it is often of course slower, but in the case just referred to the speed was very much greater ¹.

With regard to the digestion of food-material, there is no doubt that it goes on to a large extent in the inner and streaming part of the plasmodium; but that the hyaloplasm has also an absorbing power was beautifully shown in the following instance.

On February 16, 1886, I was engaged in watching Badhamia-plasmodium in a glass box, where it had remained for several days in a moist atmosphere, when I noticed on the side a dark object, probably a cluster of spores of some fungus, from which mycelium was spreading in diverging threads (Fig. 17). I saw the plasmodium advance with a clear margin of hyaloplasm from the line a in Fig. 17 to the line b, and as it encroached upon the hyphae, they instantly melted away in its transparent substance like sugar in boiling water. They left no trace beyond two small fragments of the cellulose-wall (Fig. 18, e) which remained in the hyaline medium and were never mixed up with the granular part. In this case the stimulus of the food was not powerful enough to occasion an opaque concentration of the plasmodium, which spread over the clean glass in an almost transparent film (Fig. 17, b).

The wave was arrested at the line b in the figure and soon retreated. It was then interesting to note the effect produced on the parts of the threads which had not been immersed; in the course of half an hour, there was observed a breaking-up of the cell-wall with its contents into a string of bead-like fragments for a considerable distance from the point reached by the plasmodium, and this process continued for some hours, until the chain attained the length marked in the figure (Fig. 18, c'').

¹ The question of light has nothing to do with the movements of the plasmodium of *Badhamia*; waves will spread over the sides of a glass box or a glass shade, quite indifferently whether in day or night, whether on the part exposed to full daylight or that turned to a dark corner.

I have repeatedly examined cotton wool to see if there was any appearance of absorption, but find that no change takes place, even when it has been penetrated by the plasmodium for many weeks together.

To sum up these experiments,—they indicate a remarkable power possessed by the plasmodium of Badhamia of discriminating between different foods. We find that it can be raised from a sluggish and scarcely moving condition to one of great activity by supplying it with Agaricus campestris, Boletus flavus, or with the prepared hymenial surface of Stereum hirsutum; that the coarser fibres of the latter fungus are more slowly absorbed, but that this plant is so nutritious to the plasmodium that it grows rapidly and healthily upon it.

We find that Agaricus melleus and A. rubescens, though quickly overspread, are less freely assimilated and afford doubtful nourishment; while with A. fascicularis we see that for three hours the plasmodium refused it altogether; and when at last invaded, in one instance the section was rejected and never touched again, and in the other, like a hungry man with an unwholesome meal, the creature fed, but almost died of indigestion.

We find that starch, when swollen by moderate heat, is absorbed, which is proved, not only by the manner in which the grains are eroded or disappear, but by its stimulating influence on the plasmodium, while raw starch and cotton wool are not affected1.

Again, these experiments show, that whatever may be the digestive principle of plasmodium (possibly a peptonising ferment as suggested by Krukenberg2), it is not confined to

² See De Bary, Comparative Morphology and Biology of the Fungi, Mycetozoa and Bacteria, p. 452.

¹ The spores of fungi also appear to be protected by their firm walls, and an Oidium or small pullulating fungus (Fig. 11, c, d) which always accompanies the plasmodium of Badhamia is not only uninjured, but would seem to thrive within its substance; it forms a considerable proportion of the refuse matter thrown out by retreating waves upon the sides of the moist chamber, where it multiplies with

any special part of the mass. With starch and the sections of agarics the absorption took place in the streaming interior, while in the case last related, it occurred in the hyaloplasm alone; the threads were completely dissolved in the hyaline margin, with the exception of the small fragments referred to, which were kept under constant observation until they were almost ejected by the far-retreating plasmodium.

While I have thus endeavoured to summarise the principal facts brought out by earlier observations as well as by the experience of the last twelve months, during which time the organism has remained under daily notice without a break in its constant rhythmic motion, it may not be out of place to refer to some of the negative results that have attended these investigations. I need hardly say that they afford no clue to the mystery of this rhythmic streaming any more than they explain why, at uncertain intervals of hours or days, the plasmodium will rouse up without provocation from a quiescent condition, and flow over a glass shade and then return to its former state. We may suppose that it is searching for food, but this is far from accounting for the unity of action that appears to pervade the creature.

At the risk of being tedious, I give the following note taken in February, 1887:—Plasmodium under a glass bell four inches high by four wide, crawled up the sides, completely clothing the shade with the most exquisite yellow tracery; on the following day this had changed to a loose reticulation of thicker orange-coloured veins; on adding water upon the plate beneath, the whole of the glass was in a short time covered with delicate little fans of yellow plasmodium starting from the orange veins, as it were, clothing the bare stems with leaves. I then introduced two pieces of Stereum, and in five hours the plasmodium, which for two days had overspread the shade, had almost entirely retreated and concentrated upon the Stereum.

Here we had an area of about forty square inches, covered with two or three hundred little advancing fans of plasmodium, springing from a network of branches, which was

simultaneously influenced to withdraw to the food placed upon the glass plate below.

Then again I have not been able to obtain any light on the impulse that occasions the change to sporangia. I have had a large supply of plasmodium spreading over a pile of Stereum under a bell-jar, and have removed portions into glass boxes and under glass shades, so that I have sometimes had seventeen separate colonies at one time, where the conditions of food and moisture have been apparently the same; one after another of these colonies have undergone the change, while others continued to stream. Again, the whole of the main supply has suddenly formed into sporangia, some of them suspended in clusters by yellow threads or bands, and others formed into sessile plasmodiocarps upon the plate or pieces of Stereum; the portions transferred to the smaller receptacles have meanwhile remained unaltered. On the other hand, so long as the plasmodium has been continuous, however extensive, the change to sporangia has taken place simultaneously throughout the whole 1. There is no doubt that hot weather is unfavourable to the development of sporangia, but it is remarkable that for four months not a single colony went into its final stage; though I should say that I lost a number from want of proper attention, they died and decomposed with a strong ammoniacal smell, having been poisoned by the products of the rapidly decaying Stereum. Many of the surviving colonies went into sporangia in the month of October; one which changed on the 25th seems worthy of special mention.

This was in part revived sclerotium which had dried in July. I wetted it on October 1, and it returned to active movement in the course of an hour or two; to this I added about an equal quantity of plasmodium from the store under

¹ Since writing the above, a large growth of plasmodium has formed into sporangia under a bell-jar; more than half changed on March 13, 1888, the rest on March 15. On March 11, when an appearance of sporangia occurred, I had added water, which checked the development. This plasmodium was a part of the continuous cultivation begun on Jan. 22, 1887.

a bell-jar, and the two quickly coalesced; on October 13, I fed this mixed plasmodium with *Merulius*, which it devoured, and all went into sporangia together eleven days after.

In connection with the change to sporangia I here refer to a beautiful exhibition of spore-formation which came under my notice in a specimen of *Brefeldia maxima*.

On November 27, 1887, a large mass of opaque white plasmodium was found emerging from the ground at the foot of an old fir stump. I cut off a part which had spread over some dead oak leaves, and placed it in a glass box with the cut surface against the side (Fig. 5). The piece was cushion-like in form, apparently homogeneous in substance, and closely studded with papillae. The face resting against the glass measured an inch and a quarter in length, and half an inch in height.

At ten o'clock on the following morning, the base and central part of the cut surface assumed a loose spongy texture, which, as the day advanced, became filled with air and occupied about half the area of the section.

At II A.M. a flush of pale purple appeared along the upper edge of the spongy tissue; upon this rested the broad white mass of the aethalium, composed of narrow and somewhat branching sporangia, closely cohering together and spreading radially towards the surface, where they terminated in the papillae before mentioned.

About 2 P.M. the papillae lying against the glass began to push upwards irregular and broad extensions sufficiently thin to be examined by transmitted light, and filled with remarkably large colourless granules measuring from 2μ to 4μ in diameter; the movement among these granules was extremely slow and difficult to follow, except when they poured into the pseudopodia which were here and there thrown out; no vacuoles were visible. At about 3.30 the large granules broke up into very minute bodies and numerous vacuoles made their appearance; and now for the first time the streaming movement was observed with alternate flow at intervals of about two minutes. This condition of things

continued for about half an hour. At 4 P.M. the broad extensions of plasmodium suddenly branched out from centres into clusters of short diverging branchlets (Fig. 6, a), most of which, if not all of them, contained a vacuole. At 4.30 each branchlet had constricted itself from its neighbour and taken a spherical form, the vacuoles disappeared, and the whole substance was divided into a multitude of spores (Fig. 6, d). In a few hours these had developed their spore-walls, and on the following morning had become purple-brown in colour, and in every respect resembled those which filled the sporangia. The capillitium with its strange many-chambered vesicles had already formed in the lower parts of the sporangia before any apparent change had taken place in the plasmodium at the extremities.

Brefeldia may be an especially favourable species for showing this phenomenon, on account of the extremely thin membrane which covers the sporangia, for I have never observed this free spore-formation, unconfined by any enclosing wall, in any other of the Mycetozoa.

I now return to the consideration of the resting condition referred to in the earlier part of these notes.

If plasmodium of *Badhamia*, spread on the side of a glass box, falls into an inactive state, a mottled appearance of the film is very frequently observed, which is caused by a tendency of the granules to draw together in loose groups: this passes off if the streaming revives; but if causes arise which produce greater stagnation, the concentration becomes more marked, and in process of time the aggregations are separated from each other by more or less defined hyaline spaces. When this has taken place all streaming has ceased, the plasmodium contracts to a thicker mass, and the surface is observed to be partitioned into slightly convex areas corresponding to the superficial layer of so-called sclerotium-cells which have now taken definite form.

¹ See De Bary, Comparative Morphology and Biology of Fungi, Mycctozoa and Bacteria, p. 428.

When the process is going on slowly we may sometimes notice all these stages in one lobe of plasmodium; at one extremity there may be a thin film showing streaming movement with no aggregations; then follows the mottled appearance, and further on the definite thin-walled cells may be traced, densely crowded and constituting the thick sclerotium. Sometimes a piece of plasmodium will become detached on the glass plate, and be left behind by a retreating wave, and will form into cells while all the rest continues its streaming movement.

I have had plasmodium change to the sclerotium form on wet cotton wool, but this was probably from want of nourishment. As the supply of moisture was here abundant, the margin of the sclerotium was not so abrupt as usual, and in a narrow border the cells were spread in a thin layer; many of the outermost were quite detached from the rest, and showed slow amoeboid movement.

The chief cause of the resting condition in Mycetozoa, as is well known, is lack of moisture.

When I changed my place of residence last spring, and wished to take with me the store of plasmodium which was in active state under a number of covers and in glass boxes, I removed the glass shades from those not required to be retained in the streaming condition. They at once began to form into sclerotia, and in three days were dry and ready to be packed away. After the lapse of five months, on adding water to parts of these sclerotia, the thin hyaline walls of the cells broke down and were dissolved, and in three or four hours the streaming movement returned.

On October 16, I had a rich plasmodium covering a pile of Stercum under a large bell-jar, which was inadvertently exposed for about three hours to hot sunshine. At the end of that time the whole of it had changed to fine rugged sclerotium, which I removed from the bell-jar and set aside. When portions of this were wetted again within a few days they returned to the active state in about half an hour; when

moistened, after three or four weeks, they took a longer time to recover the movement.

The dry sclerotium of *Badhamia utricularis* is dark brickred in colour, of brittle, horny texture (Fig. 7), and consolidates in irregular effused masses, which are usually made up of cord-like convolutions and knobs; the cells of which it is composed vary in size from 10 to 20 μ in diameter.

When a thin section of dry sclerotium is placed in water and examined under the microscope, the cells are seen to swell from absorption of moisture, and in a short time a slow change of position takes place in the contained granules, among which may be observed from 5 to 20 nuclei, according to the size of the cell (Fig. 8). These are not easy to detect, but if the swollen cells are carefully separated and crushed on a cover-slip, then dried and stained with magenta, the nuclei, with their nucleoli, are brought out with beautiful distinctness, especially when mounted in Canada balsam (Fig. 10).

The sclerotium is often formed with free rods connecting one part with another (Fig. 7, a); a section of one of these, when softened in water, shows very well how the refuse matter is discharged by encysting plasmodium; the outer wall of the rod is composed of mucus charged with spores of Fungi and cells of Algæ, together with other rubbish, while the enclosed cells contain only pure plasmodium.

The sharpest definition of nuclei and nucleoli which I have succeeded in obtaining has been when the cover-slips on which the plasmodium of *Badhamia* had been thinly smeared, were instantly dropped into absolute alcohol; the preparations were then stained with magenta and mounted in balsam. Stainings of hyaloplasm taken from turgid plasmodium show very few nuclei, which appear to be confined to the interior substance, for the scattered individuals that are met with were probably introduced through imperfect manipulation.

If the streaming plasmodium is examined without having resort to staining, and a morsel is placed under a cover-slip with slight pressure, the nuclei cannot at first be recognised;

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but as disintegration takes place they gradually become visible (Fig. 11, a).

They are rendered more conspicuous if a bit of plasmodium is torn with needles in a drop of water, care being taken that the cover-slip does not press too closely; viewed under a magnifying power of about 1200, the globular vesicles of finely granular plasma which ooze out from the mass are seen to contain nuclei, which are colourless and faint, but at the same time perfectly distinct in outline. They measure, as a rule, a little over 3μ in diameter, and show a clearly defined nucleolus. Occasionally a nucleus may be seen to be shot into an expanding vesicle in which none had previously appeared, as if it had formed an obstruction in the narrow passage through which the plasma issued; some globular vesicles that have become detached contain nuclei in great abundance, while others again have few or none.

When an object such as is here described has remained for half an hour or so under the cover-slip, the yellow granules will be found to have mostly disappeared, the minute granules will have more or less dispersed or congregated together, while the colourless plasma is seen crowded with nuclei throughout the preparation.

The most successful arrangement for minute observation of the streaming plasmodium is obtained when we happen to have it climbing freely over the sides of a glass shade. If this has been going on for a day or two, we frequently see little buddings out from the larger veins of delicate fans of network measuring perhaps an eighth of an inch across, or less. A drop of water is placed over one of these, and it is gently detached, with precaution that no branches are injured except the main stem, which connected it with the vein. If the little fan be placed in water on a glass slide, and the cover-slip supported at one side by a piece of blotting-paper to prevent its pressing the plasmodium, it will continue its streaming movement without interruption, and will remain in healthy condition for some days. If the fan lies in a small bubble of air surrounded by water, it will confine its movements very

much within the limits of the bubble, and will spread out in the most delicate reticulation. I have watched such an object for hours with a $\frac{1}{10}$ immersion lens, when every granule and particle of food-matter was brilliantly defined, but I have not been able to distinguish with certainty any trace of the nuclei; though when I took away the bit of blotting-paper and allowed the pressure of the cover-slip to kill the plasmodium, and water at the same time to mix with it, almost immediately the whole field was seen closely beset with well-defined nuclei (Fig. 11).

From the fact that the nuclei are invisible when surrounded with living protoplasm, it is not surprising that the process of their multiplication is difficult and perhaps impossible to observe. That the nuclei multiply with the increase of the plasmodium, there is no question. As before stated, I have cultivated large quantities of *Badhamia* plasmodium from a very small centre, and stainings taken at any time, whether on the eve of the change to sporangia, or many weeks before, are invariably found to swarm with nuclei.

In the stainings we find that, as a rule, the nuclei are of the same size, and each possesses a single nucleolus; at the same time, we not unfrequently meet with forms which suggest that division was taking place. This appearance was especially frequent in the plasmodium of *Brefeldia*, before referred to, the stainings of which were taken several days before the sporeformation occurred in the part remaining at the foot of the firstump. We notice in these forms the presence of two nucleoli taking a relative position in the two halves of the nucleus, and occasionally we meet with three nucleoli in the same nucleus (Fig. 12).

In the figure taken from stainings of *Brefeldia*, the difference in size is partly owing to the stretching of the nuclei in the thin film of plasmodium.

In concluding these notes I would just refer to the last office we see performed by the nuclei.

If a sporangium of *Badhamia*, taken about twenty-four hours after it has assumed its ultimate shape, but before the spores

have ripened, is thinly spread upon a glass slide, we find that each nucleus has collected round itself the proportion of protoplasm which would finally constitute a spore in which it stands as a centre, and each such portion has separated from those around it, or is in the act of so doing, and has become a distinct organism; for if examined at the right maturing moment these young spores may be seen in slow movement, and throwing out hyaline pseudopodia which fill with granular plasma, with the same amoeboid character which they would again exhibit when the ripe spores burst, and the new swarm-cells began the circle of development afresh (Fig. 13).

A staining taken at this stage presents a beautiful object, resembling a tesselated pavement, each polygonal area being dotted with its nucleus.

EXPLANATION OF FIGURES IN PLATES I AND II,

Illustrating Mr. Arthur Lister's Notes on the Plasmodium of Badhamia utricularis and Brefeldia maxima.

Figs. 1-4. Badhamia utricularis. Advance of plasmodium on section of stem of Agaricus melleus. 1 drawn at 12.25 p.m., 2 at 12.40 p.m., 3 at 1 p.m., and 4 at 2 p.m. $\times 3\frac{1}{2}$.

Fig. 5. Brefeldia maxima. Twenty-four hours after it was placed in glass box: spore-formation just commencing. Natural size.

Fig. 6. Brefeldia maxima. Branchings from papillae lying against side of box. a and b taken at 4.10 p.m., c at 4.20, d at 4.30, when the spore division was completed. \times 250.

Fig. 7. Badhamia utricularis. Sclerotium. × 4.

Fig. 8. Badhamia utricularis. Sclerotium-cells. × 565.

Fig. 9. Badhamia utricularis. Sclerotium-cell, stained with magenta, nuclei just discernible.

Fig. 10. Badhamia utricularis. Sclerotium-cell crushed. α part of cell-wall. b nuclei. \times 1200.

Fig. 11. Badhamia utricularis. Creeping plasmodium, pressed with water under cover-glass. a nuclei. b oil-globules. c pullulating fungus. x 1200.

24 Badhamia utricularis and Brefeldia maxima.

Fig. 12. Brefeldia maxima. Nuclei with nucleoli of plasmodium stained with magenta. × 1200.

Fig. 13. Badhamia utricularis. Young spores showing amoeboid movement, the spore a changing its form to a''' in the course of a few minutes. \times 565.

Figs. 14 and 15. Starch grains swollen in warm water, drawn from the side of glass box in which *Badhamia utricularis* was spreading. The grains in Fig. 15 have been overspread and eroded by plasmodium; those in Fig. 14 have not been reached by plasmodium. × 160.

Fig. 16. Substance dissolved by plasmodium of *Badhamia utricularis* diminishing in size as by letters, taken at intervals of about a quarter of an hour. \times 250.

Fig. 17. Mycelium growing on side of glass box. a edge of advancing plasmodium of *Badhamia utrivularis* when it first reached the mycelium. b line reached by plasmodium before it retreated. c, d threads of mycelium, which were dissolved by plasmodium between the lines a and b. \times 66.

Fig. 18. c' the thread c drawn half an hour after the plasmodium had retreated, showing the extremity breaking into bead-like fragments from action of plasmodium. c'' the same some hours after, showing extent of injury beyond the point reached by plasmodium. c'' fragments of mycelium, showing all that remained of the threads c' and c'' between the lines c'' and c'' c'' between the lines c'' and c'' between the lines c'' and c'' between the lines c'' between t



Fig. 1.

Fig. 2

Fig. 3

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Fig. 8.

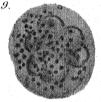
Fig. 6.

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Fig. 7.

Fig 5.

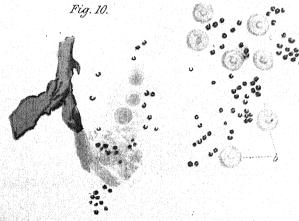
Fig. 9.



 $\widehat{f}(\widehat{A})$

a" a' a

Fig. 12.

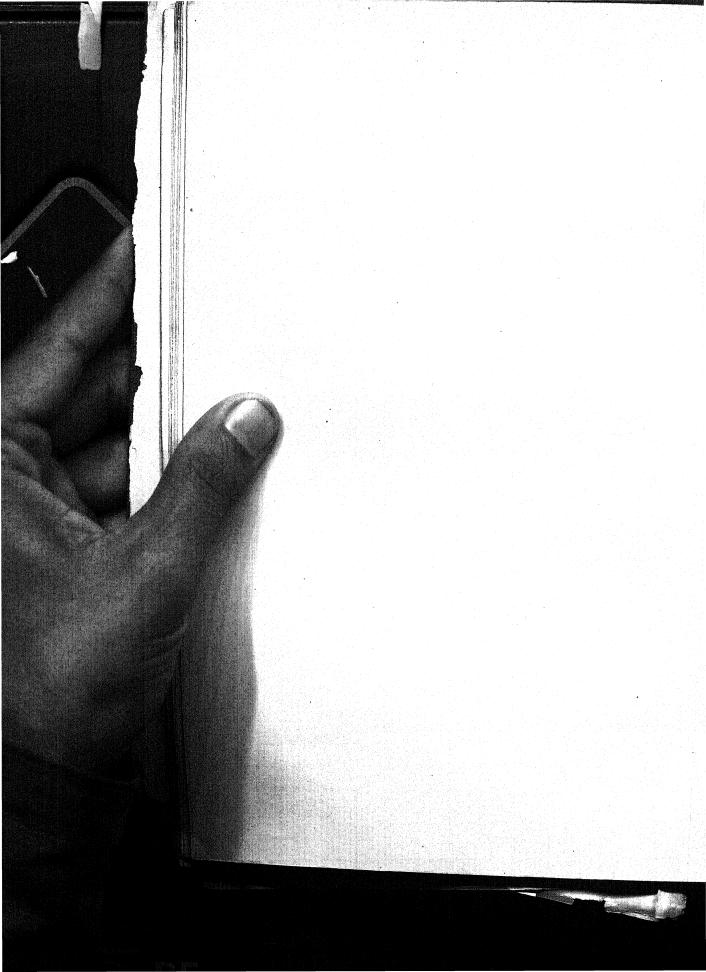


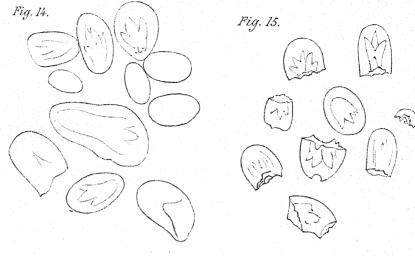
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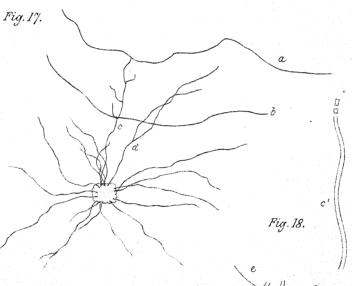
Fig. II.

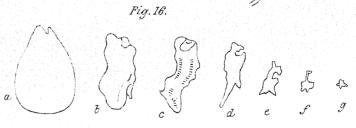
LISTER - PLASMODIUM OF BADHAMIA UTRICULARIS & BREFELDIA MAXIMA.

University Press, Oxiori.









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University Press, Oxford.

LISTER.- PLASMODIUM OF BADHAMIA UTRICULARIS & BREFELDIA MAXIMA.



A monograph of the genus Calostoma, Desv. (Mitremyces, Nees).

BY

GEORGE MASSEE.

With Plate III.

I. MORPHOLOGY.

HE presence in the Royal Herbarium, Kew, of a fine series of specimens representing the various stages of growth in Calostoma cinnabarinum, Desv. (Mitremyces lutescens. Schw.), from 8 mm. in diameter to the mature stage, has enabled me to follow the course of development from the period of differentiation of the gleba to that of dehiscence. The smallest specimen is spherical, 8 mm. across when dry, not at all attenuated towards the base, of a pale red colour, and covered with a hard, thin, translucent, wrinkled coat; which after soaking for some time in water became very much swollen and mucilaginous (Fig. 1), and on removal from the water broke away in fragments, appearing under the microscope as a structureless, colourless mass, with the exception of a thin ill-defined peripheral portion of interwoven hyphæ with thick mucilaginous walls, which, becoming more compact at the base, form there a short stem persisting after the disappearance of the upper portion.

The above structure is in every respect homologous with the peridium in the *Phalloideae*, but differs in being entirely deliquescent at an early period; hence no trace of its presence is to be seen in mature specimens. Its appearance as studied in the living condition is described as follows by the Rev.

[Annals of Botany, Vol. II. No. V, June 1888.]

Edward Hitchcock in a paper, containing many points of interest, relating to the development of the present species: 'On bursting from the soil it is enclosed in a gelatinous envelope, like *Phallus foetidus*, nearly a quarter of an inch in thickness. This immediately bursts, even before the whole body of the fungus has risen above the ground, and the exterior part of it falls upon the soil around the fungus in the form of a viscid jelly, and is ere long absorbed in the earth¹.'

The short stem-like base arises from a few firm, white, mycelium strands composed of thin-walled, sparsely septate, branched hyphæ about 4μ in diameter, the free tips bristling with minute amorphous particles of oxalate of lime. After removal of the external gelatinous volva, a vertical section shows an external colourless zone about 1 mm. thick, separated from the internal portion except at the base by a thin red line (Fig. 2). The outermost zone is composed of thick-walled mostly aseptate densely interwoven hyphæ, passing through the red zone into the central less-compact portion, where they are mixed with thin-walled, septate, branched hyphæ, having numerous slightly thickened free tips.

A second specimen, 1.5 cm. in diameter, is spherical in form, with a small obtuse umbo at the apex and abruptly attenuated below into a thick stem-like base about 0.5 cm. long, every external part being smooth and of a bright vermilion colour. The only evidence of the external gelatinous volva consists in the presence of an irregular cartilaginous ridge near the base of the stem.

When dry the plant is rigid and cuts like horn; a median vertical section in this condition shows the external wall to consist of three distinct layers, the two outermost confluent at the base, the innermost free below but in contact with the middle layer at the umbonate apex. The external layer or exoperidium is at first continuous over every part of the

¹ Physiology of the *Gyropodium coccineum*, by the Rev. Edward Hitchcock, in Sillim, Amer. Journ. vol. ix (1825), p. 56, pl. iii.

plant, about 1.5 mm. thick when dry, except at the apex where it is thinner, and increasing to 3-4 mm. when placed in water.

The red streak present in the small specimen is now seen to form the innermost portion of the exoperidium, and at the present stage of development exists in the form of red powder. In the earlier condition the cells forming the red zone are thick-walled, the substance of the walls being studded with numerous small red granules. Eventually the walls of the cells constituting this zone become mucilaginous and disappear, leaving the red granules in the form of a fine powder, thus effecting the separation of the exoperidium from the originally homogeneous spherical west of hyphæ. The innermost portion of the exoperidium consists of compactly interwoven thick-walled hyphæ about 8μ thick, not at all mucilaginous, and furnished with a few red granules which become rarer towards the outside and eventually disappear; the hyphæ at the same time becoming thinner and thinner owing to the diffluent walls, and at the outside entirely converted into a homogeneous mucilaginous jelly.

When a section of the exoperidium has been soaked for some time in water, the thin hyphæ forming the outer portion are straight, the principal branches more or less parallel and growing out towards the periphery after the manner of the palisade-tissue of a leaf, but not at all crowded and frequently anastomosing. Septa and clamp-connections are present. If a section is allowed to dry slowly under the microscope the external gelatinous portion contracts, the small hyphæ at the same time becoming spirally coiled, straightening out again on the application of water.

The red colouring matter is soluble in ammonic or potassic hydrate, agreeing in this respect with the colouring substances in *Corticium caeruleum*, *C. sanguineum*, and in the fungal element of many lichens. Owing to a slight increase in length of the basal portion between the exoperidium and endoperidium, and continued increase in size of the latter, the exoperidium is ruptured at the apex in an irregularly

stellate manner, the lobes when moistened curling inwards owing to expansion of the external mucilaginous portion, and soon breaking away at the base. The rupture of the exoperidium is described by Hitchcock as follows: 'A specimen dissected in a young state exhibits this envelope covering every part of the spherical head, with no seam discernible in it, but ere long it opens at the top, beginning to separate into numerous divisions or rays, like the opening calyx or petals of a common flower. Several valves on the top of the plant, opening into its head, are thus disclosed. A portion of the jelly, often $\frac{1}{10}$ of an inch thick, adheres to these calyx-like divisions of the envelope now under consideration, and as the inner part of it is very tender, they rarely become much expanded before they begin to coil inwards and break off at the base; merely from their weight they drop to the ground, or as is more usual adhere to the footstalk1.'

Several specimens in the Kew Herbarium show this apical splitting of the exoperidium, which is however sometimes ruptured in a circumscissile manner at or near the base, the margin splitting into irregular teeth as represented in an exaggerated manner by Nees2, who selected the name Mitremyces as expressive of the mitriform exoperidium or calyptra as it is called by Berkeley. One specimen of C. cinnabarinum and one of C. fusca (Fig 24 a) in the Kew Herbarium illustrate this mode of rupture, which is probably abnormal, as in each specimen the spores are quite mature, but prevented from escaping owing to the persistent exoperidium. In most species the exoperidium becomes completely disorganised, often remaining in the form of warts on the endoperidium, as in many species of Lycoperdon. When dry the endoperidium is cartilaginous and brittle, of a dirty ochraceous colour and less than 1 mm. thick, becoming much swollen when moistened. When young it consists of thick-walled, closely compacted hyphæ more or less gela-

¹ l. c. p. 57.

² Pilze und Schwämme, T. 11, f. 129, a.

tinous, and must be considered as homologous with the collenchyma-layer in Geaster. At a later stage the thick walls become disorganised, when a section presents the appearance of a loose west of hyphæ not more than 2 µ thick imbedded in a homogeneous mucilaginous matrix, but in reality the apparent hyphæ are the lumina of the original thick-walled cells, or more correctly the few remaining contents of the cells, as on staining with iodine the apparent hyphæ are seen to consist of minute granules forming a broken line; and from this appearance every transition can be observed in young specimens to the clearly defined thick-walled cells. Even in old specimens where the mucilage appears perfectly homogeneous in water, if the latter is replaced by alcohol, and iodine solution afterwards added, the outlines of the swollen walls are seen, owing to the accumulation of iodine in the interstices between adjoining cells, the mucilage itself undergoing no change in colour.

When young the wall of the endoperidium is of equal thickness throughout, but during the period of spore-formation, local growth takes place at the apex, resulting in the formation of an excrescence or umbo of cylindrical form, from 2-3 mm. high and the same across. The circumference of the umbo is furnished with from 5-7 deep vertical furrows situated at equal distances, so that when viewed from above the umbo presents the appearance of a 5-7-rayed star, the rays starting from a boss-like centre. At this stage a fine red streak appears in the median line of each vertical ridge separating the furrows; these streaks are continued along the apical portion of the ridge and meet in the boss-like centre. A transverse section shows that the streaks extend through the entire thickness of the wall and form a central core down the umbo, the component hyphæ undergoing disintegration similar to that already described in the red zone between the exoperidium and endoperidium. process results in the formation of an aperture or mouth, the surrounding teeth (which are subquadrate in form with a depressed central line corresponding to a groove on the wall of the umbo) remaining in apposition until the period of dehiscence, when by a process to be afterwards described, separation of the teeth takes place, the margins and inner surface of each being covered with red powder.

The endoperidium, as already stated, is not differentiated from the exoperidium at the base. There is no trace of a columella springing from the basal portion of the inner wall of the endoperidium. The innermost layer or spore-sac is at first composed of hyphæ similar to and continuous with those of the endoperidium, its external delimitation being due to gelification of the latter, the hyphæ of the spore-sac remaining unchanged. The wall is about 5 mm, thick, yellowish white in colour, flexible, and perfectly free from the endoperidium except at the apex, where it remains attached to the inner surface of the teeth; but even here it is completely differentiated, and after soaking, by the exercise of a little care it can be entirely separated, when it resembles the mouth of the inner peridium in Geaster, the teeth being very delicate and continuous with an external circular depression in the substance of the spore-sac corresponding to the portion in contact with a zone below the teeth of the endoperidium. The hyphæ on passing into the spore-sac become thinner and are loosely felted, mostly aseptate, but a few sparsely septate branches occur. During the period of spore-formation the central mass or gleba is continuous with the inner wall of the spore-sac, and consists in an early stage of densely wefted trama-like bands enclosing irregular cavities as described by Fischer1 in Sphaerobolus, but the development of this portion can only be satisfactorily studied in a complete series of living plants. The basidia are broadly obovate, measuring from $40-50 \times 15-20 \mu$, and bear five or sometimes six spores supported on minute wart-like prominences arranged in a circle round the apex (Fig. 14a). The spores are at first globose, smooth, and

¹ Zur Entwickel. der Gastromyceten (Sphaerobolus and Mitremyces), in Bot. Zeitg. 1884.

colourless, becoming eventually elliptical from $15-18 \times 8-10 \mu$, of a pale ochraceous tint, and minutely warted (Fig. 15).

When the spores are ripe, the basidia and hyphæ forming the trama become mucilaginous, the septate hyphæ breaking up into detached cells, which before complete disorganisation become very much swollen, and probably correspond to the vesicular mucilage-cells described by Fischer as occurring in the gleba of Sphaerobolus. The disorganisation extends to within about 5 mm. of the outside of the spore-sac, which now appears as a sharply defined membrane everywhere up to this period in contact with the inside of the endoperidium, but after the above-mentioned changes in the gleba contracts into a sphere less than 1 cm. in diameter, attached to the apex of the endoperidium immediately below its closed The contraction of the spore-sac is due to the peculiar behaviour of certain thick-walled hyphal constituents fixed at the point where it is attached to the teeth surrounding the orifice. These hyphæ after becoming sticky, contract in an irregular spiral manner, and draw the spore-sac with its contents up to the summit of the endoperidium. These contracted hyphæ remain for a long time unchanged in water, but if placed in dilute potassic hydrate soon begin to expand and reveal their true nature (Figs. 16, 17). There is no trace of a capillitium. The mucilage resulting from disintegration of the hyphæ contracts into irregular-shaped masses, leaving the spores perfectly free and dry in the The functional value of the various parts in connection with spore-dissemination can only be determined from an examination of living plants.

In several old specimens the spore-sac with its contents has completely disappeared from the endoperidium, and in two examples has passed through the mouth and remains attached to the teeth of the endoperidium as in *Sphaerobolus*. This extension of the spore-sac has been observed by Hitchcock and Berkeley, and may be considered as the normal mode of dehiscence, but sometimes the dry spores are forced out of the mouth without extension of the spore-sac, as described by

Hitchcock. When the dried plant is placed in water up to the mouth without allowing the inside to become wet, the endoperidium contracts from the base upwards, the teeth at the same time separating and exposing a large aperture. Until the spores are ripe the stem-like base remains small, afterwards increasing to 5–6 cm. in length by 1.5–2 cm. across, and then consists of yellowish cord-like strands of hyphæ forming a complicated mucilaginous weft when moist.

The remaining species agree in all essential points of structure with C. lutescens. There is no evidence of the presence of a capillitium in any species, the threads described by Berkeley as being present in the spore-sac of C. lurida prove on examination of the original specimens to be fragments of the trama that have not become disorganised, owing to the plant being immature when collected. The spore-sac of C. Ravenelii is described by the same author as 'entirely filling the cavity of the second peridium 1,' but this is only true of the young plant, in which it agrees with all known species; an examination of a mature specimen shows the spore-sac contracted at the apex of the endoperidium. was aware that when young the spore-sac filled the endoperidium, as in speaking of the structure of C. lutescens the following statement occurs: 'The inner peridium . . . in an early stage clearly lines the outer, and the void space arises from its ceasing to grow sooner than the outer 2.

In all species, every part of the plant with the exception of the spore-sac is perfectly rigid and cartilaginous when dry, every part with the exception of the inner surface of the endoperidium becoming swollen and more or less mucilaginous when moistened, which probably corresponds to the state of things in the living state.

The genus *Husseia* was established by Berkeley ³ from an examination of two specimens sent by Gardner from Ceylon in 1846, and he makes the following remarks on its affinities:

¹ Trans. Linn. Soc. vol. xxii. p. 130.

² Ann. Nat. Hist. vol. iii. p. 325.

³ Hook, Lond. Journ. Bot, vol. vi. p. 508, t. 17, 18, fig. 3, a, b; t. 19, fig. 1, a.

'This genus externally resembles Mitremyces, but not only is the covering of the peridium viscoso-cartilaginous, and reflected in the form of a veil, instead of falling off like a calyptra, but the capillitium exactly fills the cavity, the outer portion consisting of a barren stratum of coloured flocci, and the spores instead of being elliptic are globose and coarsely echinulate. The inner peridium is clearly represented by the barren flocci which form a dense lining to the cavity.' Both plants are figured on the plate quoted, one being immature with the exoperidium continuous, the other having the exoperidium ruptured and persistent on the stem at some distance below its apex, and the spore-sac has disappeared from the endoperidium. The immature specimen has been cut open, and shows the spore-sac filling the endoperidium.

In 1868 several more specimens of the same species were sent to Berkeley from Ceylon, one having the spore-sac extended and remaining attached to the mouth of the endoperidium (Fig. $38\,a$); two others show the spore-sac contracted as in *Calostoma*. In some specimens the stem is cylindrical, in others ventricose and slightly lacunose. The exoperidium has in every instance disappeared from the stem.

The genus *Husseia* was established before the globose-spored forms of *Calostoma* were known; but as there are now four described species of these, one of the three points of distinction between *Husseia* and *Calostoma* (*Mitremyces*) disappears; and a second relating to the spore-sac filling the cavity of the endoperidium, being only true of the immature condition, also is invalid; whilst the third point of difference supposed to be afforded by the texture and mode of rupture of the exoperidium has its homologue in *Calostoma cinna-barinum*.

The structure of *Husseia* agrees in every essential point with that of *Calostoma*. The presence of the ruptured exoperidium attached half-way down the stem is due to increase in length of the tissue between the endoperidium and exoperidium during and after the rupture of the latter. Numerous

clusters of aciculate crystals of oxalate of lime are present in the gleba (Fig. 40), and are alluded to by Berkeley as follows: 'Some parts of the flocci have at tolerably regular intervals little fascicles of bristles, the nature of which I cannot determine.'

The above statement explains why *Husscia insignis* has been placed in the genus *Calostoma* in the following arrangement. All the species referred to still exist in an excellent state of preservation in Berkeley's herbarium at Kew.

II. AFFINITIES.

Calostoma is morphologically most nearly related to the genus Geaster, the homology in many respects being absolute, the differences at the same time extreme. The external peridium of Geaster, which splits in a stellate manner when ripe, corresponds to the exoperidium and endoperidium in Calostoma, the inner peridium in Geaster being the morphological equivalent of the spore-sac in Calostoma. The outer flakey layer of Geaster, which is more or less mucilaginous in most species when young, as proved by the presence of numerous foreign particles in its substance, represents in a reduced form the universal gelatinous volva of Calostoma. The thick brown continuous layer of Geaster represents the exoperidium of Calostoma, and finally the collenchyma-layer of Geaster corresponds to the endoperidium of Calostoma.

In Geaster the morphological equivalents of the exoperidium and endoperidium in Calostoma usually remain in contact and break away as one membrane, but there are exceptions. In Geaster triplex, Jungh., the thick brown layer splits from the apex in a stellate manner, the rays becoming reflexed, whereas the collenchyma-layer remains in the form of a cup enclosing the inner peridium like the endoperidium in Calostoma. In Geaster fornicatus, Fr., the brown layer and collenchyma-layer remain in contact until after splitting into rays, when the latter separates and becomes strongly arched

upwards, remaining in contact with the brown layer at the tips of the rays. A young unexpanded *Geaster* is more or less globose and furnished at the apex with a prominence or umbo, as in *Calostoma*. A vertical section at this stage shows the external brown layer to be continuous over the apex, whereas the umbonate portion of the collenchyma-layer is fluted, as in the endoperidium of *Calostoma*.

The fluted appearance of the umbo in Geaster is due to what might be described as puckering, extending through the entire thickness of the substance, the external ridges producing corresponding internal furrows. At this period the umbo and upper portion of the inner peridium are differentiated from, but in intimate contact with, the inside of the collenchymalayer, and are as it were modelled into form during the differentiation of the latter, the external configuration of the mouth and depressed area circumscribing it, resulting, as in Calostoma, from external pressure. In Geaster the inner peridium is confluent at the base with the collenchyma-layer, in some species sessile, in others elevated on an elongated stem. This feature constitutes the most pronounced structural difference between the present genus and Calostoma. Points of minor importance are the presence of a more or less prominent columella and capillitium in Geaster.

Professor de Bary, in pointing out the connection between the *Phalloideae* and the rest of the *Gastromycetes*, says: 'The connection between *Clathrus* and *Geaster* appears to me to be still more completely established by the genus *Mitremyces*, which is chiefly American and still far from being thoroughly known. But I do not attempt to describe it here, for I have no sufficient account before me of the history of its development 1.'

This idea, which suggested the present attempt to trace the affinities of the genus under consideration, is in the main correct, although the intermediate forms necessary to prove true relationship between *Calostoma* and *Phalloideae* are not at

¹ Fungi, Mycetozoa and Bacteria, Engl. ed. p. 326.

present forthcoming, hence there is the danger of confounding analogous with homologous structures. Colus hirundinosus, one of the Phalloideae described in detail by Tulasne 1, appears to approach Calostoma most nearly in structure. This species when young is enclosed in a universal volva which is ruptured by continued growth of the receptaculum. This receptaculum is certainly analogous, if nothing more, to the endoperidium in Calostoma, surrounding the gleba, which at maturity contracts and remains suspended from the apex. The receptaculum, which is at first sessile, is not furnished with a mouth at the apex, but its lateral wall has several long slits, and the apical portion is also perforated, thus furnishing an efficient arrangement for spore dissemination by rain or insects. In the allied genera Clathrus and Ileodictyon the receptaculum at maturity resembles a sphere composed of large irregular meshes surrounding the gleba, its obvious function being that of placing the latter in the most favourable position for the diffusion of the spores, in which it agrees with the endoperidium in Calostoma, although in the latter this is effected in a different manner, as already described.

III. DISTRIBUTION.

Although the species are, with two exceptions, restricted to narrow areas, the genus is widely distributed, extending from Massachusetts (42° N. lat.) to the south of Tasmania (42° S. lat.), and from New Granada (74° W. long.) to Tasmania (174° E. long.), with a vertical range from near the sea-level to 9000 feet in the Sikkim Himalayas.

The species are divided into two natural groups characterised by the form of the spores. An eastern group, including six species with globose spores, of which C. Junghuhni may be considered the type, are distributed as follows:—C. Junghuhni,, Java, Sumatra, Ceylon, Sikkim Himalayas (8000 feet); C. Berkeleyi, Ceylon, south of the island; C. orirubra, Larut, Perak, Malay Peninsula; C. viridis, Tonglo and Sinchal,

¹ Scient. Expl. d'Algerie, Fungi, p. 435, t. 23, figs. 9-22.

Sikkim Himalayas (7000-9000 feet); C. insignis, Ceylon; C. brachystelis, Borneo and Ceylon.

The western group includes four species with elliptical spores, of which C. cinnabarinum is the type; distributed as follows: -C. cinnabarinum, east side of the United States, from Massachusetts to Carolina, New Granada, C. Ravenalii, Mountains of South Carolina; C. fusca, Tasmania and S. Australia; C. lurida, Australia (Swan River).

The close relationship of the Australian and Tasmanian with the American species has its parallel in the genus Ileodictyon, including two species not uncommon in South Australia and Tasmania, one of which, I. cibarius, has been received by Berkeley from Chili, and I have collected the same species in Ecuador at about 6000 feet elevation.

IV. CLASSIFICATION.

CALOSTOMA, Desv.

Exoperidium continuous, eventually irregularly ruptured. Endoperidium furnished with an apical toothed ostiolum. Spore-sac when young filling the endoperidium, afterwards contracting towards the apex and remaining attached to the teeth of the ostiolum. Stem composed of agglutinated cordlike strands, forming irregular reticulations or lacunae.

Calostoma, Desvaux, Journ. de Bot., vol. ii. (1809), p. 94. Mitremyces, Nees, Pilze und Schwämme (1817), p. 136. Gyropodium, Hitchcock, in Silliman's Amer. Journ. Sc.,

vol. ix. (1825), p. 56.

Scleroderma, Pers. in Desv. Journ. de Bot., vol. ii. (1809), p. 15. Lycoperdon, Bosc, in Berl. Mag., vol. v. p. 87.

The absence of information respecting the universal volva in other species than C. lutescens forbids it forming part of the generic diagnosis; nevertheless, judging from the monotypic structure of all known species in the mature condition, it may reasonably be assumed as common to all.

The remarkable diversity of appearance presented by C.cinnabarinum, Desv. (Mitremyces lutescens, Schw.) during different periods of development has been the cause of several mistakes; even Schweinitz did not know the plant in the young condition, as proved by the following statement in his Syn. Fung. Amer. Bor. in Amer Phil. Soc., 1831, p. 255:—

'1. M. lutescens, L. v. S., Syn. Car. 345; Sprengel, p. 518, rarius occurrit in Pennsylvania quam in Carolina, tamen passim.

'2. M. cinnabarinum (Calostoma), Desvaux et Brongniart, Bethl. et New York. Satis affine Mitremyci—sed peridium externum, corneum, coccineo-cinnabarinum, primum omnino clausum, demum deciduum et revolutim fissum in lacinias. Stipite prioris.'

It is evident that the above new species of Schweinitz is the young condition of his own *M. lutescens*. It is not quite clear whether the above specific character is original or a quotation; if the latter, I have not been able to trace it. Further, Schweinitz does not appear to have been acquainted with Desvaux' original generic diagnosis, or that of the species (*M. lutescens*, Schw.) on which it was founded, as Brongniart is not mentioned in any way. The following is the description as given by Desvaux ¹:—

'Calostoma, Sclerodermate spec., Pers.

'Pediculus coriaceus, lacunoso-clathroideus; peridium globosum, cortice duplici; exteriore coriaceo, apice aperto dentato persistenti, dentibus marginato-reflexis appropinquatis; cortice interiore tenuissimo, pulvere copioso luteo filis multis intermixto.

'Calostoma cinnabarinum, Scleroderma calostoma, Pers. page 15 du 2º vol. de cet ouvrage, pl. 2, fig. 2.

'Pediculo lacunoso; peridio globoso dilute purpureo, 4-7 dentato.

'Habitat in America boreali, supra terram.

'Obs. Cette plante est quelquefois décolorée, lorsqu'elle, a été desséchée sans précaution, parceque sa couleur, qui est seulement extérieure et ne pénètre point dans le tissu de l'écorce, extérieure du péridie, est formée par une espèce de Pruine rouge, susceptible de se détacher.'

Observations sur quelques genres à établir dans la famille des Champignons, par N. A. Desvaux, Journal de Botanique, vol. ii. pp. 94-95.

The above incontrovertibly proves that the plant described by Desvaux is the same as *Mitremyces lutescens*, Schw.; hence

Calostoma, having priority, must replace Mitremyces.

Persoon's figure quoted by Desvaux is very characteristic of the plant intended, whereas the same cannot be said for the figure of Nees, which does not represent a real plant, yet, as the species of this genus are not generally known to mycologists, a preconceived idea is formed from the last-named figure.

Calostoma Junghuhni (Schl. et Müll.), Mass. Plate III, Fig. 21.

Exoperidium ochraceous, with sometimes a greenish tinge, soon breaking up into irregular warts, which persist for some time on the broadly elliptical ochraceous endoperidium, mouth vermilion, teeth 4–6, erect at first. Spore-sac pale, spores globose, coarsely tuberculose, pale ochre, 14–18 μ diameter, stem-like base composed of more or less parallel mycelial cords above, ending in a thickened mass of finer interwoven strands.

Mitremyces Junghuhni, Schlechtendal et K. Müller, in Bot. Ztg. 1884, p. 401, Taf. iii. B.; Sacc. Syll. v. 7. n. 204.

M. Beyrichii, Sch. et Müll., l.c. Java (Junghuhn), Sumatra (Junghuhn), Sikkim Himalayas, 8000 feet (Dr. G. King).

Variable in size, endoperidium ·5-1·5 cm. high; stem-like base 1-2 cm. long. In some specimens the warts of the exoperidium are persistent, in others disappearing at an early stage of development, leaving the endoperidium smooth externally.

Calostoma Berkeleyi, Mass., n. sp. Plate III, Fig. 33.

Exoperidium ochraceous externally, inside reddish brown, ruptured irregularly at the apex and breaking away, leaving the subglobose, ochraceous endoperidium smooth; ostiolum vermilion, teeth 5, acute, erect. Spore-sac pale, spores globose, minutely verruculose, very pale ochre, $7-9\,\mu$ diameter, stemlike base ochraceous, irregularly lacunose.

Mitremyces lutescens, Schw., Berk. in Herb. (Type in

Herb. Berk. Kew, n. 4472). Ceylon, south side of the island (Gardner, n. 673).

Superficially resembling *C. lutescens*, to which species it was referred by Berkeley and Broome in their enumeration of the fungi of Ceylon in Linn. Soc. Journ. vol. xiv. p. 78, but readily distinguished by the globose spores. It differs from *C. Junghuhni* in the smaller and less coarsely warted spores and in the structure and colour of the exoperidium.

Calostoma orirubra, Cooke. Plate III, Fig. 31.

Fasciculate. Exoperidium dark brown, soon broken up into large persistent pointed warts. Endoperidium broadly ovate or elliptical, ostiolum vermilion, teeth 4–5, erect and forming a cone before expansion. Spore-sac pale ochre, spores spherical, coarsely tuberculate, very pale ochre, 14–17 μ diameter. Stems confluent, forming a subglobose lacunose brown mass.

Mitremyces orirubra, Cke. in Hb. Kew. (Type in Hb. Kew.) In a cluster on the ground. Larut, Perak, Malay Archipelago. (Dr. King.)

Endoperidium 1-1.5 cm. high, studded with prominent brown-pointed warts. Growing in clusters of three or four together, the confluent stems forming a knob 2-3 cm. across. A very distinct species, most nearly allied to *C. Junghuhni*.

Calostoma viridis (Berk.), Mass. Plate III, Fig. 29.

Exoperidium in the form of dingy green irregular scales adhering to the subglobose pale green endoperidium, ostiolum vermilion, teeth 5–7, sub-acute, erect and forming a cone before expansion; spore-sac pale, spores globose, closely tuberculose; very pale ochre, $12-15\,\mu$ diameter. Stem-like base, stout, greenish, irregularly lacunose.

Mitremyces viridis, Berk., in Hook. Kew Journ. Bot. vol. iii. (1851), p. 201; Ic. Plant. pl. 869, f. B. (type in Hb. Kew); Sacc. Syll. v. 7. n. 207. On the ground and on dead timber. Tonglo and Sinchul, Sikkim Himalayas, 7–9000 feet. May, June, rare. [Dr. (now Sir Joseph) Hooker, with fig.]

A very beautiful and well-marked species, the whole plant

of a dull green colour. Endoperidium about 2 cm. in diameter. Stem 2 cm. or more long by 1–1·5 cm. thick. Its nearest affinity is with *C. orirubra*.

Calostoma insignis (Berk.), Mass. Plate III, Figs. 35, 36.

Exoperidium ochraceous, broken into irregular lobes, which sometimes remain attached to the middle of the stem-like base. Endoperidium, smooth, ochraceous, ostiolum pale green, teeth 5–8, erect. Spore-sac pale green, spores globose coarsely spinulose, pale ochraceous, $14-17\mu$ diameter. Stem-like base cylindrical or ventricose, smooth or lacunose.

Husseia insignis, Berk. in Hook. Lond. Journ. Bot. vol. vi, p. 508, Tab. 17 and 18, f. 3, a, b, Tab. 19, f. 1, a (1847); Sacc. Syll. v. 7. n. 200. (Type in Herb. Berk. Kew, n. 4478.) Adam's Peak, Ceylon; and south of the island (Gardner), Borneo.

Endoperidium 1.5-2 cm. diameter, stem-like base 3-4 cm. long by .5-1 cm. thick when ventricose.

C. pachystelis (Ces.), Mass.

Exoperidium thick, irregularly ruptured, and persistent at the base of the stem. Endoperidium globose, mouth umbonate, furnished with teeth.

Husseia pachystelis, Cesati, Mycetum in itinere Borneensi lecti ab O. Beccari descrip. p. 13, with fig.; Sacc. Syll. v. 7. n. 201. Sarawak, Borneo (Beccari).

The largest species of the genus. Exoperidium nearly 1 cm. thick, from 5–7 cm. across when ruptured; endoperidium little more than 2 cm. in diameter; stem 4–5 cm. long by 1·5–2 cm. thick, internally lacunose, externally furrowed. Evidently a good *Calostoma*; the spore-sac appears to have disappeared from the endoperidium in the mature specimens, and is represented as filling the cavity of the latter in the section given by Cesati, which is evidently an immature plant with the thick exoperidium still continuous over the endoperidium, and Cesati says, 'Gleba sporifera totum peridium replens in fungo juvenili vel adhuc clauso.' No mention is made of the form of the spores, which, judging from affinity and locality, were presumably spherical.

Calostoma cinnabarinum (Desv.) Plate III, Figs. 6-8.

Exoperidium vermilion inside, becoming dingy red, separating at the base like a calyptra, or breaking into irregular lobes at the apex. Endoperidium subglobose, ochraceous, ostiolum vermilion, teeth 5–7. Spore-sac very pale ochre, spores elliptic-oblong, minutely verruculose, pale ochre, $15-18\times8-10\,\mu$. Stem-like base variously lacunoso-reticulate. Desvaux, Journ. de Bot., tom. ii. (1809), p. 94.

Gyropodium coccineum, Hitchcock, Sillim. Amer. Journ.,

vol. ix. (1825), p. 56, pl. 3.

Lycoperdon heterogeneum, Bosc, in Berl. Mag., v. p. 87, t. 6, f. 10 α , b.

Lycoperdon callostoma, Poir, Encycl. suppl., v. 476.

Scleroderma callostoma, Pers., in Desv. Journ. de Bot., vol. ii. p. 15, pl. 2, f. 2.

Mitremyces heterogeneus, Nees, Pilze und Schwämme, p. 136, t. xii, f. 120 a (1817).

Mitremyces lutescens, Schweinitz, Syn. Carol. n. 345, t. 2, f. 1; Nees, Syst. der Pilze, Pl. 11; Fr. S. M. 3. 64; Sacc. Syll. n. 202. Mitremyces cinnabarinum, Schw. Syn. Fung. Amer. Bor. in Amer. Phil. Soc., p. 255 (1831); Exs. Ellis, N. Amer. Fung. n. 727; Sacc. Syll. 7. n. 208; the Kew copy contains a beautiful specimen in the young state, with the bright red exoperidium continuous, and the stem-like base rudimentary. (Specimen from Schweinitz, in Hb. Bk., Kew¹.) On the ground. United States, New Granada. Endoperidium 1-2 cm. in diameter; stem 2-5 cm, long, 1-2 cm. thick.

Calostoma Ravenelii (Berk.), Mass. Plate III, Figs. 26, 27. Exoperidium becoming broken up into irregular warts, which often remain attached to the subglobose, ochraceous, endoperidium; mouth vermilion, teeth 4–5; spore-sac pallid, spores elliptic-oblong, smooth, colourless, $15-17\times8-9~\mu$. Stemlike base, short.

Mitremyces Ravenelii, Berk. in Trans. Linn. Soc., vol. xxii.

¹ The bracketted reference indicates the value and locality of the specimen from which measurements, drawings, &c. have been taken.

(1857), p. 130, tab. 25 B; Sacc. Syll. 7. n. 203. (Type in Herb. Berk., Kew, n. 4473.) On the ground, Caesar's Head; mountains of South Carolina (Ravenel).

Endoperidium 5-1 cm. in diameter; stem-like base less than I cm. long. Berkeley's measurements are in all instances taken from dried specimens, and consequently rather smaller than mine, which are taken from specimens that have been moistened. Agreeing with *C. lurida* in size, and in the smooth elliptical spores.

Calostoma fusca (Berk.), Mass. Plate III, Fig. 24.

Simple or caespitose. Exoperidium dark brown externally, dingy red within. Endoperidium pale brown, subglobose, ostiolum vermilion, teeth erect, and forming an umbo before expansion, 4–6 in number. Spore-sac white, spores ellipticoblong, minutely verruculose, pallid. Stem-like base stout, elongated, brown, costato-lacunose.

Mitremyces fuscus, Berk. in Ann. Nat. Hist., vol. iii. (1839), pp. 325-326, Pl. vii, f. 1; Sacc. Syll. v. 7. n. 206. (Type in Herb. Berk., Kew, n. 4474.)

Mitremyces australis, Berk. in Herb. Tasmania (Archer), (Gunn); near Melbourne, Australia (Berggren); Lake Muir, Australia (Muir).

Solitary or in clusters, two or three springing from a common base. The whole plant is of a dark brown colour, endoperidium from I-I·5 cm. in diameter, stem-like base 2-3 cm. long by I cm. thick. Most nearly allied to *C. lutescens*, with which it agrees in the mode of separation of the exoperidium.

Calostoma lurida (Berk.), Mass. Plate III, Fig. 19.

Exoperidium breaking up early into small blackish granules, which remain attached to the ochraceous, subglobose endoperidium; ostiolum black internally, as well as the margins of the 4-5 teeth. Spore-sac pale ochre or whitish, spores ellipticoblong, smooth, pallid, $16-20 \times 7-9 \mu$. Stem-like base short, brown, irregularly lacunose.

Mitremyces luridis, Berk. in Hook. Journ. Bot., vol. iv. (1845),

pp. 65, 66, tab. 1, f. 5; Sacc. Syll. v. 7. n. 205. (Type in Herb. Berk., Kew, n. 4475.) On sandy soil, Swan river, Australia (Drummond).

In the text Berkeley has called the above species *M. luridis*, on the plate it is called *M. lucidus*, and in the description of the plate *M. luridens*, hence three names are given to the plant in

the original description.

The exoperidium disappears very early, the small persistent wart-like remains showing little or no structure. Endoperidium about 1 cm. in diameter; stem-like base 1 cm. or less in length, and evidently more or less mucilaginous when growing, as it is studded with firmly imbedded grains of sand, and fragments of various kinds. Allied to *C. Ravenelii*, but readily distinguished from this and every other known species by the black ostiolum.

EXPLANATION OF FIGURES ON PLATE III,

Illustrating Mr. Massee's Monograph of the genus Calostoma, Desv.

Fig. 1. Very young specimen of *Calostoma cinnabarinum*, showing the mucilaginous external volva, a; and the cord-like mycelium, b. Nat. size, after being soaked for some time in water.

Fig. 2. Vertical section of Fig. 1, after removal of the volva; the thin red line is the commencement of differentiation of the exoperidium. Nat. size.

Fig. 3. Transverse section of Fig. 1. Nat. size.

Fig. 4. Older specimen of *C. cinnabarinum*; the volva has disappeared and the exoperidium is continuous over every part. At this stage the spores are mature, but the spore-sac still completely fills the endoperidium. Nat. size.

Fig. 5. Transverse section of Fig. 4; α , exoperidium; b, endoperidium; c, sporesac; d, gleba. Nat. size.

Figs. 6, 7, 8. Mature condition of *C. cinnabarinum*; a, remains of exoperidium; b, endoperidium; c, spore-sac extruded. Nat. size. 6, drawn from a dry specimen; 7, 8, after soaking in water.

Fig. 9. Ostiolum of Fig. 7. x about 10 diam.

Fig. 10. Diagrammatic representation of the structure of the umbo in vertical section; a, exoperidium; b, endoperidium; c, core of red tissue that eventually becomes disorganised and forms the centre of the ostiolum passing vertically through the umbo of the endoperidium; d, spore-sac; c, ostiolum and surrounding portion of spore-sac which remains in contact with the endoperidium after contraction of the lower portion.

Fig. 11. *C. cinnabarinum*, section through exoperidium, a; endoperidium, b; and spore-sac, c; d, mucilaginous matrix towards outside of exoperidium; e, a few spores that have become mixed with the hypha forming the spore-sac. \times 400 diam.

Fig. 12. Portion of a thread from the red zone between exoperidium and endoperidium during the first stage of disintegration, indicated by the appearance of numerous minute red granules in the substance of the wall. × 700 diam.

Fig. 13. Hypha showing clamp-connections from exoperidium of *C. cinna-barinum.* × 400 diam.

Fig. 14. Basidia with spores of $\it C.~cinnabarinum,~a,~rudimentary~wart-like$ sterigmata. $\times~400~diam.$

Fig. 15. Free spores of C. cinnabarinum, showing the various forms. \times 400 diam.

Fig. 16. Portion of one of the coiled hypha that cause the contraction of the inner peridium in $C.\ cinnabarinum.$ \times 400 diam.

Fig. 17. Same as Fig. 16, after being treated with dilute potassic hydrate. \times 400 diam.

Fig. 18. Portion of mouth and upper portion of spore-sac of *C. cinnabarinum*, showing teeth, α ; and depressed circumscribing zone, b. \times about 4 times.

Fig. 19. C. hurida. Nat. size (after being moistened).

Fig. 20. Spores of Fig. 19. x 400 diam.

Fig. 21. C. Junghuhni. Nat. size (after soaking).

Fig. 22. Vertical section of C. Junghuhni; a, endoperidium; b, spore-sac contracted. Slightly enlarged.

Fig. 23. Spores of C. Junghuhni. \times 400 diam.

Fig. 24. C. fusca; at a, the exoperidium shows the circumscissile mode of rupture. Nat. size (after soaking).

Fig. 25. Spores of C. fusca. × 400 diam.

Figs. 26, 27. C. Ravenelii in different stages of development. Nat. size (moistened).

Fig. 28. Spores of C. Ravenelii. × 400 diam.

Fig. 29. C. viridis. Nat. size (after being moistened).

Fig. 30. Spores of C. viridis. \times 400 diam.

Fig. 31. C. rir bra. Nat. size (moistened).

Fig. 32. Spores of C. orirubra. × 400 diam.

Fig. 33. C. Berkeleyi. Nat. size (moistened).

Fig. 34. Spores of C. Berkeleyi. × 400 diam.

Figs. 35, 36. C. insignis; a, ruptured exoperidium. Nat. size (moistened).

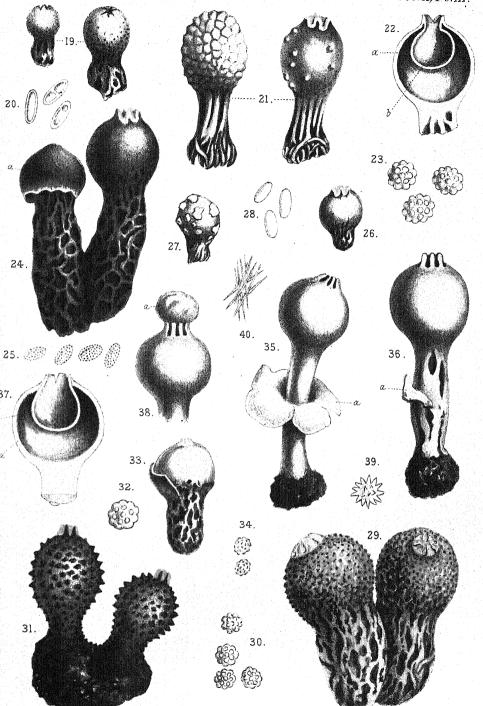
Fig. 37. Vertical section of C. insignis; a, endoperidium; b, spore-sac in contracted state. Slightly enlarged.

Fig. 38. C. insignis; endoperidium with spore-sac, a, extruded. Nat. size.

Fig. 39. Spore of C. insignis. × 400 diam.

Fig. 40. Cluster of acicular crystals of oxalate of lime from gleba of C. insignis. \times 700 diam.

Annals of Botany 13. 🕫 12. A Mary Same 18. 16. 11. G. Massee del. MASSEE.- ON CALOSTOMA.



University Press, Oxford.



On the presence of sexual organs in Aecidium.

BY

GEORGE MASSEE.

With Plate IV. A.

TROMYCES Poae, Rab., is considered by Winter1 as a stage of the Aecidium found on Ranunculus Ficaria. The former is rare with us, having been hitherto only recorded from two districts, whereas the latter is probably the commonest and most universally distributed of any member of the genus. In the Royal Herbarium grounds at Kew it is very abundant, but no trace of the Uromyces has occurred, although carefully looked for throughout the season, which led to the idea that, like Puccinia graminis, this Aecidium might possess some means of reproducing itself independent of the Uromyces. During the past spring, while looking for mycelium in 'healthy' leaves of R. Ficaria obtained from plants having the Aecidium present on other leaves, I noticed in one section a spherical weft of interlaced hyphae, the tip of one thread situated in the centre of the mass ending in a clavate head, rich in coarsely granular protoplasm (Fig. 1). The section was kept alive for several days, during which the clavate body increased in size, its protoplasm becoming less granular, several highly refractive globules appeared, and staining with methyl-green demonstrated the presence of a well-defined nucleus with a nucleolus. The mycelium found in the leaf agreed in every respect with that of the Aecidium, and was traced down the petiole and into the tubers. I cannot say

¹ Kryptogamen-Flora (Pilze) p. 162. See also Rab. in Univ. itin. 1866, No. 38. [Annals of Botany, Vol. II. No. V, June 1888.]

whether the mycelium originated in the leaf from germinating spores of *Uromyces* and passed down the petiole into the tubers, or spread from the latter into the leaf, but it will be shown later on that, when the spores germinated, they sent germ-tubes into the tubers of the *Ranunculus*.

Being desirous of ascertaining whether the clavate body mentioned above was in any way connected with the Aecidium, numerous young unopened peridia were cut, but without result, as when the presence of the parasite is manifested by elevation of the leaf-epidermis, even before the latter is ruptured by the peridia, the weft of mycelium has undergone important changes; and it was not until I had made sections through those portions of the leaf first showing traces of the fungus in the form of a slight discoloration or the appearance of spermogonia, that I discovered the clavate body in a ball of mycelium which represented the initial stage of an Aecidium. In this instance the object of search was in a more advanced stage (Fig. 2), clearly showing it to be an oogonium, accompanied by an antheridium. The oogonium was much larger than the one first seen, in form irregularly oblong, measuring about $50 \times 25 \mu$, terminal on a thread from which it was cut off by a transverse septum, and containing finely granular protoplasm with numerous refractive globules. I could see no trace of a nucleus without reagents, which I did not apply, being desirous of observing the development as long as possible. The antheridium is cylindrical, about 40 \times 12 μ , and like the oogonium filled with protoplasm and oil globules and termianted by a short lateral branch, springing from a thread distinct from the one supporting the oogonium, so far as I could trace the two in the mass of mycelium. The antheridium is cut off from its supporting hypha by a transverse septum. The point of contact between the antheridium and oogonium was on the side turned away from the eye, so that I am unable to state the exact manner in which fertilisation is effected. After remaining for two days in water with 2 per cent. of glycerine, the antheridium became empty and shrivelled; the oogonium during the same period having in-

creased in size and assumed a broadly obovate outline (Fig. 3). The hypha supporting the oogonium and immediately below it gave origin to a considerable number of lateral branches which grew up round the oogonium, and, along with the original west of hyphae, forms the external covering of interlaced threads enclosing the peridium during its development. On the third day the oogonium collapsed, when methyl-green revealed the presence of several small nuclei. The next phase of development consists in the oogonium becoming coarsely nodulose (Fig. 4), each nodule, with the exception of the basal row, eventually developing into a thick cylindrical basidium from the apex of which spores are cut off in succession by transverse septa, the oldest at the apex, the youngest at the base. The basal row of nodules develops like the others, but the adjacent rows of cells are agglutinated together and form the peridium (Fig. 5), which after dehiscence is reflexed, the component rows again separating from each other at the free margin. The growth of lateral branches below the oogonium after fertilisation recalls to mind what takes place in Peziza, as shown by Tulasne¹, and also in the Florideae, whereas the development of a protective organ from the oogonium itself is rare, if not without parallel. The spores are capable of germination the moment they become free in the peridium, and when placed in a damp atmosphere send out one, rarely two, germ-tubes, which may remain simple, but generally produce several lateral branches. The whole of the protoplasm and orange colouring matter passes from the spore into the germtube (Fig. 6). Spores sown on sections of tubers of Ranunculus Ficaria germinated, the tubes entering the tissues of the tuber. Tulasne has pointed out2 that when the spores of Aecidium ranunculacearum are sunk in water, they do not germinate so readily as when placed in a damp atmosphere. During the past season, at the end of May, I placed a quantity of leaves bearing the Aecidium in question in a bottle

¹ Ann. Sci. Nat. sér. 5, Tome vi, p. 211, pl. 11-12.

² Sur les Urédinées et les Ustilaginées, in Ann. Sci. Nat. sér. 4, Tome 2,

containing water, where they remained until the third week in July, when on examination I found the spores still remaining in the peridia apparently unchanged, and on being placed in a damp growing-cell germination took place in a very peculiar way. On the thisd day most of the spores were filled with broadly elliptical colourless bodies, measuring about $6 \times 4 \mu$; some had already escaped, the remainder following, accompanied by a cloud of granules and disintegrated ectoplasm when the spores were placed in water (Fig. 7); the whole process resembling very much what takes place in the germinating spores of Spumaria alba, Bull., only in the present instance the escaping bodies exhibited no spontaneous movements, neither could I detect the presence of cilia. Further experiments with the remaining material corroborated the above observations in every particular, with the exception in one instance of a suspicion of movement, but too vague to justify the term zoospores being given to the bodies in question. I have reasons for believing that a shorter period of submergence suffices for the production of the above method of germination, as I have detected similar bodies in the spores of herbariumspecimens, the peridia of which had probably been flooded with water for a short period and collected before the spores discharged their contents. In Phytophthora, according to De Bary1, the mode of germination varies from a germ-tube to the production of zoospores, depending on the nature of the solution in which the gonidia are placed.

¹ Fungi, Mycetozoa, and Bacteria (Engl. ed.), p. 109.

EXPLANATION OF FIGURES IN PLATE IV, A.

Illustrating Mr. G. Massee's paper on the presence of sexual organs in Aecidium.

Fig. 1. Young oogonium of Aecidium ranunculacearum. × 400 diam.

Fig. 2. Oogonium and antheridium of same. × 400 diam.

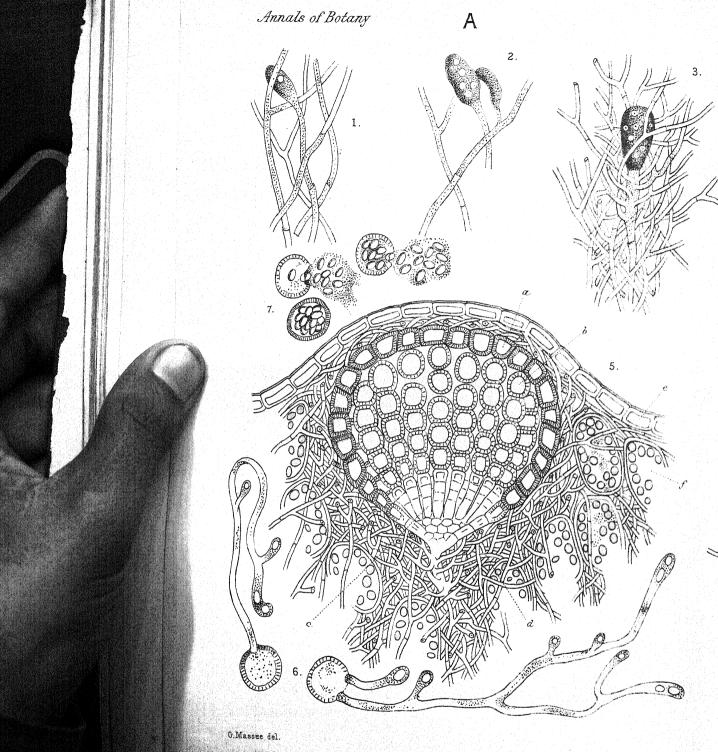
Fig. 3. Oogonium of same after fertilisation; with hyphae growing from the hypha supporting the oogonium. × 400 diam.

Fig. 4. Oogonium of same at a later stage of development, showing the prominences which form basidia and peridium respectively. × 400 diam.

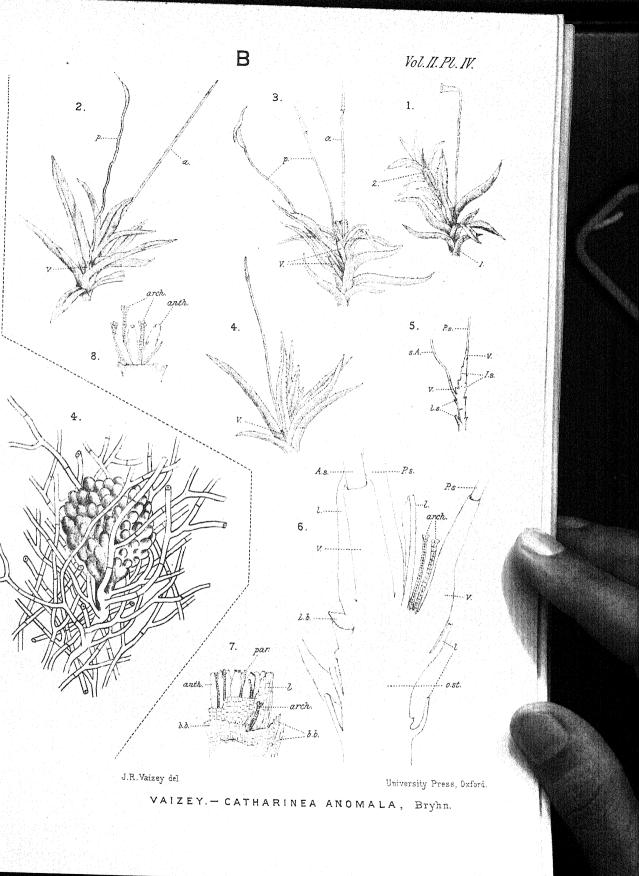
Fig. 5. Young plant of same before rupture of peridium: a, peridium; b, aecidiospores; c, basidia; d, external covering of hyphae, some of which originate from the hypha supporting the oogonium, others from the original weft accompanying the oogonium; e, epidermis of leaf, as yet unbroken by the parasite; f, cells forming mesophyll of leaf. \times 400 diam.

Fig. 6. Aecidiospores of same germinating. × 500.

Fig. 7. Aecidiospores of same, germinating after having been under water for several weeks, and afterwards placed in a damp atmosphere. × 500 diam.



MASSEE.— SEXUAL ORGANS IN ÆCIDIUM.





On the formation of sugars in the septal glands of Narcissus.

BV

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With Woodcuts 1, 2, 3, 4, 5, and 6.

THE nectaries of *Narcissus* belong to the class known as septal glands or inner nectaries, which constitute one of the most remarkable examples of the specialisation of tissues for a definite function to be met with in the vegetable kingdom, and are consequently well suited for a study of the changes which occur during secretion.

Septal glands are only known to occur in monocotyledonous plants; they were first described by Ad. Brongniart in 1855.

The best account of the general nature of these organs is by Grassman², which deals chiefly with the occurrence and rough anatomy of septal glands. The author gives a detailed list of all the natural orders and genera in which nectaries of this form have been observed, and also an account of their development³. With regard to the latter point Grassman arrives at the general conclusion, 'Die Septaldrüsen entstehen durch teilweise Nichtverwachsung der Fruchtblätter in den Septen.' All my observations on the young stages of the ovary in Narcissus Tazetta, L., and N. pseudonarcissus, L., show that this statement holds good for Narcissus.

¹ Ann. des Sc. Nat., sér. 4, tom. ii. 1855.
² Flora, lxvii (1884).

³ Cf. sect. B. of his paper, Entstehung der Septaldrüsen.

[Annals of Botany, Vol. II. No. V, June 1888.]

The well-known papers of Bonnier¹ and Behrens² on the whole subject of floral nectaries contain scattered allusions to septal glands; but neither author devotes special attention to them. Full details of all the literature devoted to this subject are to be found in the works of Bonnier, Behrens, and Grassman. Stadler³ describes the structure of certain septal glands.

I selected *Narcissus Tazetta*, L., and *N. pseudo-narcissus*, L., for observation in preference to other plants containing septal glands for the following reasons: the protoplasm of the cells is only slightly coloured; the tissues in the early stages at least are moderately free from tannin; the gland-cells are comparatively large.

The ovaries were cut into small pieces and preserved in absolute alcohol without any previous treatment, as this was found to be the most satisfactory method of fixing the protoplasm. Dilute solutions of picric or chromic acid (.5-2 p.c.) also gave good results; but where there is little tannin present absolute alcohol is decidedly to be preferred. All the observations on the protoplasm were made from sections of material preserved in this way; but in testing for sugars at the different stages described below fresh tissue was used, the ovaries taken being as nearly as possible the same size as those preserved in alcohol from which the sections were cut. Details as to the method of treatment before observation are given in the explanation of the figures. In the observations as to the nature of the free cell-walls bordering on the lumen or cavity of the gland use was made of 3-25 p.c. solution of aluminium chloride in absolute alcohol, to clear the sections before staining; this reagent was found to cause no swelling-up of the cell-wall provided the alcohol was perfectly anhydrous, whereas alcoholic potash, strong enough to clear the tissues, caused the cellulose structures to lose their sharp outline.

In speaking of the sugars in liquid secreted by the glands,

Les Nectaires, in Ann. des Sc. Nat. 1878-79.
 Die Nectarien der Blüthen, in Flora, Ixii (1879).

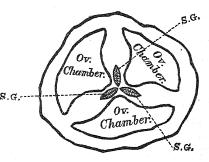
Beiträge zur Kenntn. der Nectarien und Biologie der Blüthen. Berlin, 1886.

I use the term glucose to denote any soluble carbohydrate which reduces Fehling's solution immediately, and saccharon for those which reduce the same only after inversion. There is unfortunately a good deal of confusion as to the use of these terms 1, but I wish to point out that the term as used below is to be taken, not as signifying a definite substance sucro-dextrose, but any member of the class of glucoses; thus, 'invert sugar' and even maltose might be included under the term as used here.

Cane-sugar, sucrose, or saccharon, is the only substance capable of inversion likely to be present, and where the term is used below it can fairly be regarded as synonymous with cane-sugar; but here again I only intend the term to stand for any member of the class of saccharons as defined above.

Before proceeding to the account of changes in the secreting cells I give a brief description of the general structure of the glands in Narcissus.

In the genus Narcissus² there are three separate glands: one in each septum of the ovary, not united in the centre and simple; they only occupy s.g. the upper part of each septum not extending below the middle of the ovary. The ducts are short and they open into the base of of the glands.



straight, widening somewhat at the free end where pseudonarcissus, L.; showing general position

the floral tube (Fig 1). The tissue of the septa is loose, with large intercellular chambers, but becomes close towards the centre in which

¹ See Armstrong and Groves, in Miller's Elements of Chemistry, Part III, § 1, p. 649. London, 1880.

² Compare Grassman on Crinum asiaticum, taf. i. 11-13, and Stadler, loc. cit.

the glands are situated. The fibrovascular tissue is conspicuously developed in the close small-celled septum-parenchyma surrounding the epithem of the glands.

The cavity is straight and narrow, widest in the central portion of the gland, prolonged upwards into the short straight duct, and gradually diminishing in width towards the lower extremity, till the epithelial cells become almost contiguous.

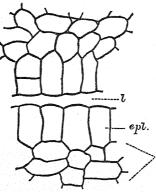


Fig. 2. Narcissus Tazetta, L. Transverse section, showing structure of the gland shortly before opening of flower, from a section mounted in dilute glycerine, treatment for three hours before staining with 10 per cent. aluminium chloride in thelium; e. epithem.

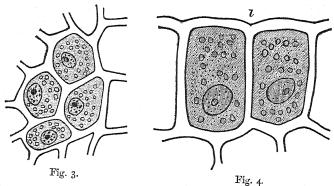
The epithelial cells are somewhat elongated, entirely contiguous laterally, but rather irregular in shape and size; the free walls bordering on the cavity are more or less arched outwards, and show no traces of cuticle; they are of the same thickness as the lateral walls and stain perfectly uniformly with chlorzinc-iodide and methylene blue (Fig. 2).

Several layers of well-marked epithem tissue invest the epithelium on the inner side; and stained with methylene blue, after those next the epithelium are considerably smaller than the absolute alcohol; l. cavity; epl. epi- cells of the septum-parenchyma; but the outermost layers

pass gradually over into the ordinary septum-tissue; there is no endodermis or distinct line of demarcation between the epithem of gland and the surrounding parenchyma. The epithem-cells are more or less angular and fit closely without any intercellular spaces, whereas the surrounding tissue is very loose. The connection of the fibrovascular bundles with the epithem tissue is very evident; some of the branches run entirely in the epithem, and endings of the usual nature can be observed at intervals. Other branches run with one side contiguous to the epithem and the others

surrounded by the septum-parenchyma; every variety of intermediate stage between bundles which run completely in the epithem and completely in the septum-parenchyma may be observed.

It is interesting to note here that it follows from Grassman's account of the development of septal glands that the epithelium is true epidermal tissue, although the epithem is derived from the fundamental ground tissue; and that in these structures we find an instance of epidermal cells taking on a secretory function also assisted by the adjacent hypodermal layers, as is so frequently the case in vegetable secretory structures.



Figs. 3, 4. Appearance of protoplasm in the epithem and epithelium cells of gland of *Narcissus Tazetta*, L. before formation of sugar, from transverse section of a young bud. Mounted in glycerine and alcohol after staining with borax-carmine; from material preserved in absolute alcohol. *I.* position of gland-cavity.

W. Gardiner¹ compares the structure of nectaries to that of chalk-glands occurring in Saxifragaceae and Crassulaceae, and this is especially noticeable in the case of septal glands; but it must be remembered that the physiological significance of the two cases is quite different, as chalk-glands only excrete in virtue of the activity of root-pressure, whereas the secretion in nectaries is entirely independent of the same.

If a transverse section through the upper part of the ovary

¹ Proc. Camb. Phil. Soc., vol. v, pt. i, and Q. J. Mic. Sci., vol. xxi, N. S.

of a young flower bud, before the gland-cells have reached their full size, be examined under a high power, the protoplasm of the epithelium and epithem-tissue appear as shown in Figs. 3 and 4.

The cells are completely filled with protoplasm having no vacuoles; they contain a large conspicuous clearly-defined nucleus, and numerous small roundish or irregularly-shaped granules of a proteid nature; the proof that these granules are of a proteid and not carbohydrate or resinous constitution is given in full below. At this stage the cells contain no sugar or substances which reduce Fehling's solution even after treatment with dilute acid to 'invert' any saccharons which might be present.

These observations may be made on sections mounted in dilute glycerin or glycerin and alcohol, but are much more easily observed when the sections are stained with borax-carmine or Hoffmann's blue, especially if the latter be used dilute so as to colour the protoplasm only and not also the cell-wall. Haematoxylin and ammonia-carmine also show the structure well if used dilute.

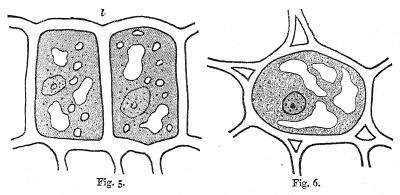
In the older buds, where the gland-cells have reached their maximum development, but still some time before the opening of the flower, small vacuoles can be observed in the protoplasm, and the number of granules rapidly diminishes with the advancing age of the cells. At this stage small quantities of sugar can be detected in the cells by the Fehling test; an immediate red precipitate of cuprous oxide is obtained on dipping the sections in the boiling reagent, which shows that glucose is present; but the precipitate is markedly more copious if the sections are allowed to remain for some time in the reagent, or are previously treated with dilute acid, to cause inversion of any saccharons, showing that saccharon is present in addition to glucose.

In the next stages the vacuoles rapidly enlarge, the granules

¹ See Roscoe and Schorlemmer, Treatise on Chemistry, vol. iii, pt. ii, 'Cane sugar,' London, 1884; and Armstrong and Groves, loc. cit.

disappear almost entirely, and the outline of the nucleus becomes less distinct. Glucose and saccharon are now abundant in all the cells, and can also be detected in the cavity of gland and duct, if very thick sections are used.

I was not able to ascertain accurately at what stage the sugars are first passed into the cavity, because any sugar in solution in the cavity is immediately washed out on placing in the hot Fehling's fluid; for this reason a section taken across the ovary, even when the flower is open and the gland-cavity and duct consequently filled with saccharine liquid, does not appear to contain any sugars. If, however, very thick sections be used, a few particles of cuprous oxide can generally be observed in the cavity adhering to the walls; but such appearances are by no means a trustworthy indication, as they might easily be derived from the contents of the surrounding cells which have been ruptured.



Figs. 5, 6. Appearance of protoplasm in the epithelium and epithem cells of a gland of a fully open flower of *Narcissus Tazetta*, L. Same treatment as in case of Figs. 3 and 4.

I may here notice that neither at this nor any other period during the activity of the glands could I detect any sugars in the intercellular spaces of the surrounding septum-parenchyma, and that as a general rule the epithem cells next the same contained much less sugar than those nearer to the epithelium.

Little further change takes place in the protoplasm of the cells after this till the opening of the flower. Figs. 5 and 6 may be regarded as showing the structure of one of the cells at the period when the secretion is being most actively poured out.

The nectariferous secretion first makes its appearance in the floral tube some time before the opening of the flower, but how long before seems to vary greatly with the rate of growth even in flowers of the same plant. After the flower is fully open further changes rapidly take place in the gland cells, the vacuoles increase largely in size, all the granules disappear, and oil-drops begin to be formed in the now diminished protoplasm (Figs. 5 and 6). Tannin was first observed in the vacuoles at this stage (by the iron and chromic acid reactions), and the cell-sap is more distinctly acid than in earlier stages. No starch-grains or solid matter giving a carbohydrate reaction with iodine, or chlor-zinc-iodine, could be detected in any of the stages, nor do any of the dextrins which colour with iodine (erythrodextrins) seem to be present.

The gland-cells appear to contain sugar even after the withering of the perianth, but after tannin begins to be copiously formed, it is very difficult to draw certain inferences from the reaction with Fehling's solution, as many varieties of tannin readily reduce the fluid. The subsequent changes in the cells were not followed out in detail, as they have no connection with the formation of sugar, but it may be stated here that, owing to the rapid increase in size of the septa after withering of the perianth, the epithem and epithelium cells split away from one another, and the cell-walls quickly lose their distinct outline, and undergo a mucilaginous degeneration.

In the mature capsule the positions formerly occupied in the septa by glands are indicated by small cavities with a more or less ragged outline containing fragments of cellulose and mucilage attached to the lining cell-walls.

Observations on the gland-cells in Nothoscordum bulgaricum, Lindl., Ornithogalum nutans, Lk., and Allium sp.? appear to confirm the results described for *Narcissus*, but I hope to publish shortly a comparative account of the changes in the allied plants.

The reactions of granules in the protoplasm, which prove them to be of a proteid nature, are, that with boraxcarmine they stain more deeply than the mass of the cellprotoplasm, though not so darkly as the nucleus. Hoffmann's blue they stain as the surrounding protoplasm. If the sections are overstained so that the re-agent also colours the cell-walls, the granules appear darker than the surrounding protoplasm. In common with the surrounding protoplasm they show the xantho-proteic reaction when treated in the usual way with nitric acid and ammonia. They do not show any swelling up with water or dilute acids, but are easily soluble in 5 to 8 per cent aqueous potash. In alcoholic potash weaker than 10 per cent, or in aluminium chloride than 3 per cent., they do not alter, but protracted exposure (8 to 12 hours) to concentrated solution of either re-agent causes their gradual disappearance. With iodine in potassium iodide, iodine and sulphuric acid, chlor-zinc-iodine, or tincture of iodine, they only assume a yellow or brownish colour, and show no trace of blue or violet. Rosolic acid (corallin) with sodium carbonate gives no distinct coloration. They are not altered by alcohol containing 3 per cent. of ether benzene, or petroleum spirit (therefore not of a resinous or fatty nature). If sections of the fresh tissue be mounted in water or dilute glycerin, the granules do not show any indication of the 'starch-grain crossing' with polarised light.

The sections with which these reactions were tried were all, except in the last case, where fresh tissue was used, taken from material preserved in absolute alcohol, without any previous treatment.

When thin sections of the fresh tissue were placed in absolute alcohol I was not able to observe in any cases a separation of the saccharon crystals in the cells, probably the quantities present are too small to allow this to take place, although

saccharon is said to be almost completely insoluble in cold anhydrous alcohol.

In the formation of glucose ¹ from starch or cellulose, dextrins are always formed simultaneously during the early stages of the reaction, whether the change is brought about by the agency of diastase or of artificial reagents, and the dextrins first formed (e.g. erythrodextrin) give a reddish colour with iodine. Now, as stated above, no substance showing the reactions of an erythrodextrin was detected at any stage in the cells, and I consider that the absence of such, especially at the time when the sugars can first be detected, is of some value as evidence that the glucose is not formed by hydrolysis of a carbohydrate.

Although there is evidently a close connection between the groups of saccharons and glucoses, cane-sugar has not been artificially prepared by any reaction, and it does not seem possible to obtain it by any simple process from starch or cellulose. Maltose 2 , a carbohydrate having the formula C_{12} H_{22} O_{11} , is easily obtained from starch, etc., but differs greatly in its properties from cane-sugar.

The conclusions I should draw from these experiments as to the nature of the process of secretion of sugars in *Narcissus* and other plants having the kind of nectaries called septal glands, are:—

- 1. That the first stage consists in a maximum formation of protoplasm containing a large amount of metaplasm, especially in the form of proteid granules, but not of starch-grains, mucilage, or any form of solid carbohydrate.
- 2. That the sugars are probably derived from the decomposition of this metaplasm, and constitute one of the products of the change. That both glucose and saccharon are formed simultaneously.
 - 3. That the excretion of the saccharine liquid 3 into the

¹ See O'Sullivan, Journ. Chem. Soc. xxix. 479, and xxx. 126; Brown and Heron, in Journ. Chem. Soc. xxv. 618. Musculus and Gruber, Comptes Rend. 86, 1459; Roscoe and Schorlemmer, loc. cit.; Armstrong and Groves, loc. cit.

See O'Sullivan, loc. cit.; and Schultze in Ber. Deut. Chem. Ges. vii. 407.
 Compare Wilson in Unters. Bot. Institut, Tübingen, 1881; and Gardiner, loc. cit.

gland-cavity in the first instance takes place through the cell-walls (which are not cuticularised) without any rupture, splitting away of the cells of epithelium from one another, or mucilaginous degeneration, and must therefore be supposed to result, in the first instance at least, from the direct activity of the protoplasm in the secreting cells.

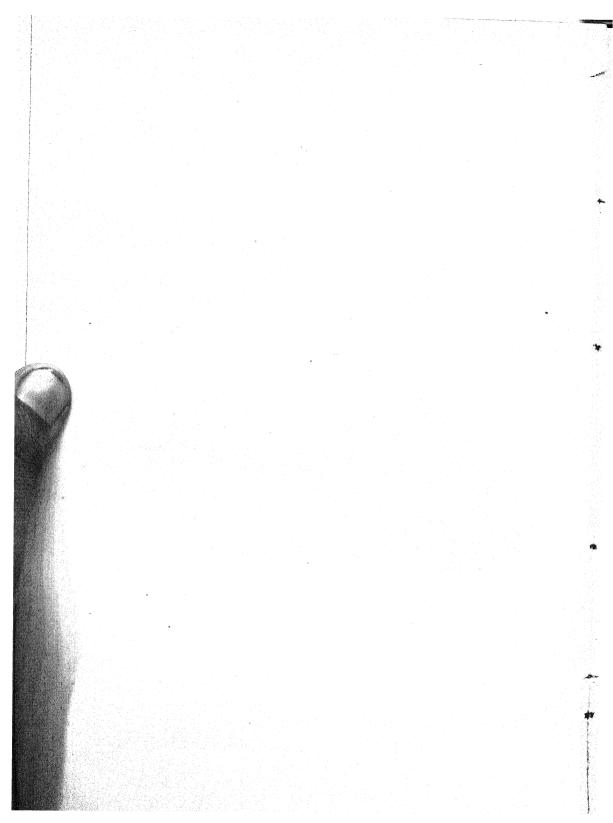
Finally, I should wish to call attention to the close analogy between the results deduced from these observations and those of W. Gardiner 1 on the secretion of mucilage in the hairs of Blechnum occidentale and Osmunda regalis, and especially to his remarks on the similarity of the process of secretion in its general features by animal and vegetable protoplasm.

I think also that the formation of sugars in this manner may be regarded as comparable to the formation of cellulose from microsomata ², and of starch from amyloplasts ³ in its general nature, but in such a comparison it must be remembered that the formation of solid products, such as mucilage, starch, cellulose, etc., from specialised portions of the protoplasm admits of direct proof, whereas it is hardly possible to obtain more than indirect evidence in the case of soluble bodies, such as sugars.

¹ Annals of Botany, vol. i, No. 1.

² See Vines, Phys. of Plants, p. 25-26, Cambridge, 1885.

³ See Vines, loc. cit. p. 26 and 180.



On a method of studying Geotropism.

BY

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AND

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I T is commonly assumed, in accordance with the teachings of Sachs, that the gravitation-stimulus which produces geotropic curvatures acts most strongly when the geotropic organ is placed horizontally. In other words, when an organ is placed obliquely, it is in a less favourable position for the development of geotropism than when it is horizontal¹.

On the other hand, Elfving² has given evidence to show that in the case of roots the position of maximum effect is when the apex of the root is directed vertically upwards, i.e. when the organ is at 180° from its normal position.

Our inquiry on this question is far from complete, and is published rather as pointing out a new method of attacking the problem, than as by any means solving it.

The subject is one on which it is difficult to obtain satisfactory evidence. Thus, if we compare two negatively geotropic organs placed obliquely, so that the free end of one of them is above, while that of the other is below the horizon, we are at once confronted with a well-known difficulty. Assuming that the horizontal is the position of maximum effect, we must suppose that the stem which is beneath the horizon, and which therefore approaches the

¹ See Sachs, Arbeiten, ii. p. 240, i. p. 454. Flora, 1873, p. 326.

² Acta Soc. Scient. Fennica, 1880. The question is discussed by Vines in his Phys. of Plants, p. 460.

[[]Annals of Botany, Vol. II. No. V, June 1888.]

horizon as it curves upwards, is exposed to an increasing stimulus. In the same way the stem, starting from above the horizon, curves away from the optimum position, and thus encounters a stimulus diminishing in a similar ratio. It is clearly therefore extremely difficult to find out what were the initial geotropic tendencies corresponding to the two positions. The difficulties inherent in this experiment made it seem desirable to apply to the question a method differing from those hitherto employed.

If a flower-stalk (or other apogeotropic organ) remains for an hour or two pinned down to a board in a horizontal position, so that no curvature can take place, a well-known result is seen on its being released:—the freed end springs up with a sudden geotropic curvature. Our method is based on this fact. Geotropic stems were immoveably fixed at various angles, and the amounts of curvature occurring on release were taken as representing the geotropic stimulus corresponding to each position. Whatever may be the faults of the method, it has one merit, namely, that the organ is exposed to a *constant* instead of to a *varying* stimulus, as must be the case if the stem is free to curve during the period of stimulation.

Sachs¹ has compared shoots constrained in this manner in a horizontal position, with shoots fixed at one end only, and therefore free to move from the first. He shows by an analysis of the distribution of growth and tension, that the curvatures in the two cases are of an essentially similar nature. These results encourage us to believe that we are right in drawing conclusions as to normal geotropism from the behaviour of constrained shoots; for we do not consider the difference pointed out by Sachs between the two classes of curvature sufficient to vitiate our method.

Our experiments were made in the following manner:-

Young flower-stalks of plantain (*Plantago lanceolata*) were gathered, and after the removal of the flower-heads were pinned on to boards. This was not done by transfixing

¹ Arbeiten, i. p. 204.

the stalks, but by using a pair of crossed pins at each point which it was desired to confine. In this way every stalk was attached at both ends and in the middle. The boards were then placed in a tin box containing damp sand. One board was placed horizontally, and the others at angles of 60°,—in one case with the apical end of the stalk upwards, in the other downwards. The three sets may be distinguished as Above, Below, and Horizontal. The box was placed in a damp chamber at a constant temperature of 25°C, for two hours. The stalks were then released and placed in water for an hour, during which time the curvatures materially increased¹. The form assumed by each was recorded by tracing2 the curvature on paper. The amount of curvature was measured by taking, from the tracings, the angle between the older and younger parts of the stalks. This could be done by drawing tangents to the curves, and was found more satisfactory than estimating the radius of curvature in each case.

The following table gives the results of experiments, made in June 1887, on 148 plantain stalks. The whole series of angles is given, in order that the great amount of inequality in the results may be seen.

ABOVE: 39°, 27°, 38°, 33°, 37°, 32°, 30°, 35°, 57°, 41°, 28°, 32°, 43°, 46°, 35°, 30°, 27°, 44°, 30°, 35°, 62°, 90°, 34°, 77°, 39°, 82°, 90°, 39°, 81°, 30°, 47°, 30°, 33°, 31°, 60°, 29°, 45°, 54°, 63°, 41°, 40°, 28°, 52°, 56°, 23°, 15°, 46°, 33°, 56°, 15°. Average of 50 angles=
$$42.8$$
.

Average of 46^3 angles= $43\cdot 1$.

¹ The stalks were placed on their sides in a flat-bottomed vessel, so that the increase of curvature was due to after-effect, not to a continuance of geotropic stimulation.

² The form was traced with a fine paint-brush, by which means a more trust-worthy representation of the curvature can be made than with a pencil.

³ Omitting one which remained straight.

HORIZONTAL:
$$47^{\circ}$$
, 67° , 45° , 50° , 56° , 82° , 51° , 62° , 54° , 67° , 51° , 67° , 66° , 58° , 35° , 43° , 45° , 45° , 36° , 48° , 59° , 78° , 64° , 48° , 57° , 74° , 75° , 67° , 60° , 63° , 50° , 50° , 45° , 64° , 58° , 71° , 70° , 56° , 60° , 45° , 81° , 74° , 63° , 32° , 74° , 75° , 89° , 90° , 34° , 44° , 55° .

Average of 51 angles = 58° 4.

In spite of the want of uniformity, the results are sufficiently clear when the averages are compared.

				AVERAGE ANGLE.	OR AS
Horizon	ITAL			58·4°	100
ABOVE		4.		42.8°	73:3
Below	•	•,	•	43·1°	<i>73</i> ·8

From these figures we get some idea of the amount of difference in geotropic tendency between horizontal and oblique stems. Having regard to the want of uniformity in the angles, it would not be safe to suppose that the averages represent the difference in question with any kind of accuracy. But they certainly confirm the belief that the horizontal position is the most favourable for geotropic stimulation.

The results with plantain were confirmed by a few experiments (three sets of 12) made with flower-stalks of the cabbage. Here the average angles were:— OR AS

				W8-C	o were.	010 110
Horizon	ΓAL		• .		52.7	100
ABOVE		;-• ?	••	•	33.2	63.0
BELOW .			•		39•8	75.5

We do not attach any importance to difference between the *Aboves* and *Belows*, because the number of experiments is too small to allow of trustworthy conclusions. But the experiments with cabbage, like those with plantain, certainly give additional support to the belief that the horizontal is the *position* of maximum effect.

DEPARTMENT OF BOTANY, UNIVERSITY OF ALLAHABAD.

On Catharinea lateralis, Vaizey (Catharinea anomala, Bryhn). A new British Moss.

RV

J. REYNOLDS VAIZEY, M.A.

With Plate IV, B.

In the autumn of 1886 I found several of what I believed to be anomalous specimens of Catharinea undulata, differing from typical C. undulata by possessing lateral fruits either in the place of or in addition to the normal terminal fruits. These specimens I unfortunately lost.

I happened to mention the fact of my finding this anomalous form to Professor Lindberg, of Helsingfors, who informed me that the same or a similar anomalous form had been discovered and described by Dr. N. Bryhn¹ as a new species, under the name of *C. anomala*.

As Bryhn's description is very brief and without figures, I propose to describe and figure the new species, if such it be, giving at the same time some of my observations of new facts in regard to it.

From the information we have at present, it may be concluded that the distribution of the form extends over at least the north of Europe and Asia. Professor Lindberg tells me, in a letter dated December 13, 1887, that specimens were collected by Dr. Arnell in 1876 near the river Jenisei in Siberia ². In May, 1886, Dr. Bryhn discovered it near Skien,

¹ Bryhn, *Catharinea anomala*, n. sp. in Botaniska Notiser, 1886. Häftet V, p. 157.

² In a letter dated December 30, 1887, Dr. Braithwaite writes that 'some thirty-five years ago' he found a plant with all the appearance of the form I am now to describe near Snaresbrook in Essex; but he did not keep the specimen.

in Telemarken, in Norway, and subsequently in other localities in the south of Norway. In October, 1886, I first found it at Broxbourne, in the county of Hertford, and again in October, 1887, and I have seen it frequently since in other localities in the same neighbourhood.

This form is distinguished by bearing sporogonia laterally on the stem of the oophyte in the axils of the leaves, in addition to the sporogonium borne at the apex of the oophyte-stem (Figs. 2, 5, and 6). There may also be more than one lateral fruit on the same stem, and each of the additional ones may be produced in the axil of the same leaf as the first, or in that of another (Fig. 3). I have in some specimens even found a young partially developed embryo of a third. It is probable that this would develop later, as some of the specimens which I have in my possession gathered by Dr. Bryhn, dated May 26, 1886¹, have some sporogonia still immature; and in one specimen I have found three mature lateral setae in addition to the single terminal one. Bryhn mentions as many as five altogether. Sometimes lateral fruits only are developed, as shown in Fig. 4.

In the majority of specimens that I have examined the sporogonia appear to be formed in archegonia, fertilized in acropetal succession, the lateral fruit being the youngest. In some few specimens this was not the case, the oldest being that furthest from the apex; and in one or two no order acropetal or basipetal could be recognised.

The lateral fruits differ from the terminal constantly, or almost constantly, in having a distinctly flexuose and slightly thinner seta; in many the flexuose character is very marked, in only a few it is hardly perceptible.

The arrangement of the antheridia and archegonia presents considerable variations. In all the Scandinavian specimens which have been examined the inflorescence has been described as *autoicous*. In my English specimens three different con-

¹ These specimens were kindly sent me by Professor Lindberg from his herbarium.

ditions have been observed. In some specimens I have been unable to find any antheridia at all. It is, of course, possible that, as at the time the specimens were examined they were in fruit, the antheridia had in some specimens decayed or been destroyed, though I think this unlikely1. These specimens were therefore dioicous. In other specimens antheridia were found in the axils of the leaves in considerable numbers, but without any archegonia with them, the archegonia in this case being found in the axils of other leaves; the plants were therefore autoicous. In others, again, antheridia and archegonia were found mixed in the axil of the same leaves, a synoicous condition. Unfortunately I did not note down each specimen as I examined it, and consequently I cannot give any figures to represent the proportions of dioicous to autoicous and synoicous specimens. My impression is that autoicous and synoicous are both rather more numerous than dioicous; the autoicous and synoicous being about equal in number. I did not examine enough specimens to form a really just estimate of the proportion of the different arrangements; not more than thirty specimens were dissected altogether.

I have not been able to make out any difference in the structure of the leaf from that found in *C. undulata*.

Besides the form just described, certain other variations from the normal Catharinea-type have been found. In some specimens I have found two terminal fruits growing from the *same inflorescence. This variation is, I believe, fairly common, and has, I think, been recorded before. I have observed it in other mosses, e.g. Dicranum scoparium and Polytrichum formosum, Hed. A variation that I have not before seen noticed is one represented in Fig. 1, which I have seen twice at least. On the one year-old oophyte stem, with a terminal fruit, an innovation is produced immediately below the 'floral' axis.

¹ It curiously happens that in all the specimens I sent to Professor Lindberg and to Dr. Braithwaite which they examined they failed to find any antheridia.

In this way a sympodium is formed on which the fruit comes to have an apparently lateral position.

I have found two specimens cladocarpous, the oophyte stem having sent out a lateral branch, on the end of which there was a sporogonium, as well as on the main stem. I have also one specimen in which the lateral branch has a lateral fruit. Through the kindness of Mr. J. G. Baker, of Kew, I learn that in the Kew Herbarium a cladocarpous form occurs as *C. undulata* under Desmaziere's Crypt. France, Series I. No. 250. I find that Milde 1 described and named a form as *Atrichum anomalum* in 1869 quite different from that now described; consequently, in conformity with usage, the name of Bryhn must be discarded as having been previously occupied. I therefore propose, after having consulted with Dr. Braithwaite, to call the present form, whether it be regarded as a variety or species, *C. lateralis*.

As we have no absolute criterion of species and variety, I shall not discuss in which category the present form should be placed. I am rather inclined myself to regard it as an incipient species.

With the knowledge of the existence of such a form as that just described, and of the pleurocarpous species of *Fissidens* among acrocarpous mosses, it is impossible not to think a classification founded upon the difference between acrocarpous, cladocarpous and pleurocarpous mosses, a highly artificial and unnatural one. If this view be adopted, it may be hoped that it will be a step towards the discovery of a new and more natural system of classification for the mosses.

BOTANICAL LABORATORY, CAMBRIDGE, February, 1888.

¹ Bot. Zeit. 1869, and Jaeger et Sauerbeck, Genera et Species, Muscorum.

EXPLANATION OF FIGURES IN PLATE IV, B.

Illustrating Mr. J. Reynold Vaizey's paper on Catharinea lateralis.

Fig. 1. Catharinea, with terminal fruit having an innovation arising just below floral apex.

Fig. 2. C. lateralis, with terminal (a) and lateral (b) fruit.

Fig. 3. C. lateralis, with two lateral fruits (p). The vaginula (v) is shown in both.

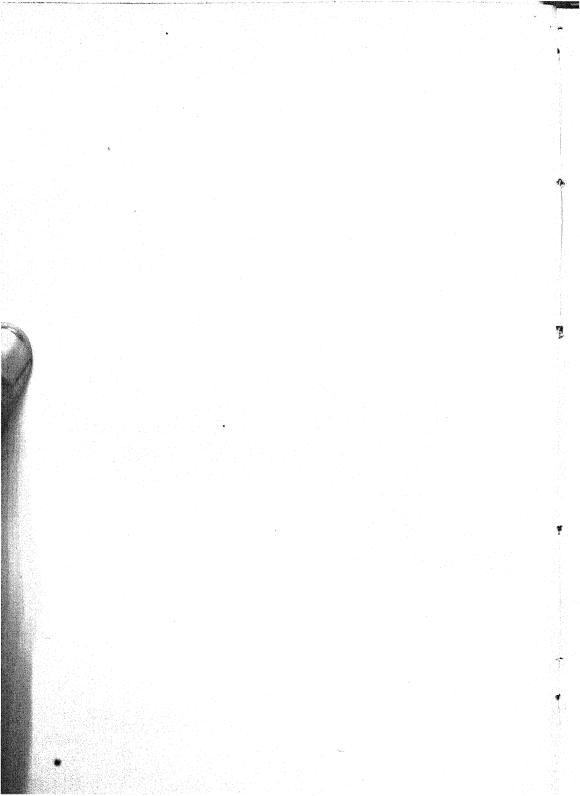
Fig. 4. C. lateralis, having a lateral fruit, but without a terminal fruit.

Fig. 5. C. lateralis, with leaves dissected off to show truly lateral position of lateral fruit: A. s. terminal fruit; P. s. lateral fruit; v. vaginula; l. s. leaf bases.

Fig. 6. Median section, to shew relation of setae to leaves, &c.; letters as in Fig. 5: leaf; o.st. oophyte stem; arch. archegonia.

Fig. 7. Male flower from autoicous specimen, with part of a female flower just below: ℓ . leaf; ℓ . ℓ . leaf-base; anthr. anthridia; arch. archegonia. The specimen from which this was drawn had two or three mature setae.

Fig. 8. Synoicous flower: letters as in Fig. 7.



MANAGESTAN OF ALLANGARD,

On the Structure, Development, and Affinities of Trapella, Oliv., a new Genus of Pedalineae.

RV

F. W. OLIVER, B.A., F.L.S., Scholar of Trinity College, Cambridge.

With Plates V, VI, VII, VIII, IX, and Woodcut 7.

IN a collection of plants received at the Kew Herbarium I from Dr. Augustine Henry, from central China, in February of last year, there were, along with many other new and interesting plants, some specimens of a bilabiate aquatic with curiously appendaged fruits and inferior ovary. This plant, recalling in habit and in its appendaged fruits the well-known Trapa natans, was made by my father the type of a new genus, Trapella, with specific name sinensis. It is described and figured in the 'Icones Plantarum',' and placed provisionally in the Order Pedalineae. Amongst the observations made upon it there is the following:- 'The form of the ovules remains uncertain, the stigma is very curious and of, as yet, uncertain structure, and there are one or two other features of biological interest that we want more light upon.' The possession of these marked peculiarities—unintelligible without proper investigation of material preserved in alcohol and, if a true Pedalinea, its exceptional habit, made it desirable that further material should be obtained. On this account Dr. Henry was communicated with, the result being that in

¹ D. Oliver, in Hook. Ic. Pl. 1595.

[Annals of Botany, Vol. II. No. V, June 1888.]

the autumn of 1887 a sufficient supply of spirit-material of this plant arrived from China.

This was handed to me for more complete and detailed investigation; and in the present paper are given the results of my research, carried out during the past winter.

That I am able now to give this monographic account of a plant unknown to science before 1887, speaks to Dr. Henry's prompt courtesy in obtaining and dispatching material. No Botanist in China of recent times has sent home collections richer in entirely new forms than has Dr. Henry, who is now working at the flora of central China, hitherto an almost sealed book.

Trapella (for general view of the plant, see Pl. V. Fig. 1) is an aquatic Phanerogam with long straggling and simple or sparingly branched stems, which ascend obliquely through and float at the surface of the water. At intervals of from 40-50 mm. opposite leaves are borne, deltoid-rotundate, and without stipules. Their petioles always twist so that the lamina of the leaf is parallel to the surface of the water. The lower, submerged leaves differ from the floating ones; they are oblong. The internodes in this region also are much longer than in the upper part of the stem. The lower ends of these shoots would appear to arise from a system of horizontal thread-like rhizomes which grow at the surface of the mud and give off several such ascending branches. Many adventitious roots arise from the nodes of these submerged parts, and sometimes even from the internodal regions. In this way the plant is anchored to the bottom (Fig. 2).

In the axils of the floating leaves, and of the submerged ones for some distance below the surface, flowers are formed, which in the former case open just above the surface, but in the latter are cleistogamic. Generally speaking, flowers are not produced in both the leaf-axils at one node, though in some cases this is so, and both may develop into fruits (V. Fig. 1). Ramification of the ascending axes is not frequent; when it occurs it is from the axil of a submerged

leaf, and often the shoot formed remains insignificant (as in Fig. 1).

The bilabiate corolla has, Dr. Henry says in his note accompanying the material, a limb pale blue above, passing into a tube below which is yellow both outside and in I. It would appear that only one flower is in bloom at once on any shoot. After the corolla has fallen away five spines arise below, and alternating with, the calyx-lobes. These spines give the fruit an extremely characteristic appearance; and this, taken with its floating habit, has led the Chinese, Dr. Henry informs us, to speak of the plant (from its resemblance to *Trapa*) as *t'ich ling-chio*, i. e. 'iron Trapa'; the adjective 'iron' indicating the uselessness of the plant, in contrast to *Trapa* itself, which is of great value economically. The word seems to be used in a sense analogous to that in which we use 'dog,' e.g. dog-rose, etc.

The plant grows in 1-2 feet of water in a pond in the neighbourhood of Ichang, in the province of Hupeh; and the material which has been investigated by me was gathered July 18th-21st last—less than nine months ago at the time of writing.

Soon after the first material of *Trapella* was received at Kew, M. Maximowicz of St. Petersburg received from a correspondent at Tokio, Japan, fragments, which though insufficient to describe, rendered it probable that it was at any rate a species of our genus. On the strength of this I hunted through the illustrated Japanese plant-books in the Kew Library, and in volume 76 of the beautiful 'Phonzo Zoufou,' devoted to aquatics, occurs a coloured hand-drawing ² of a plant, undoubtedly belonging to our genus,

¹ In his memorandum accompanying the first received dry specimens, Dr. Henry speaks of the corolla as being white above, so that the shade of blue is probably very faint.

² In this figure a floating stem only, with fruits, is drawn; no flowers are given, nor any of the submerged oblong leaves. The leaves are rather more deeply cut than in our plant, and adventitious roots are represented arising from nodes at which are inserted floating leaves. The fruits, though fancifully drawn, belong undoubtedly to *Trapella*.

and likely enough is the same as that of which M. Maximowicz had a fragment. I am indebted to Mr. Atsushi Matsura, a Japanese gentleman at present studying at University College, London, for a translation of the remarks accompanying the sketch in question, of which the substance is here given: 'Hishimodoki'—the Japanese name of the representative of our genus—'is brought from Owari or Bishiu' (an eastern province of Japan). 'The plant comes into leaf in the spring; its leaves are of small size, resembling those of Trapa incisa¹; they are arranged in rows opposite one another, and roots originate at the side of every node of the plant. In the autumn it produces a fruit betwixt leaf and stem (i.e. in the leaf-axil), in form resembling an anchor or long-legged spider. The plant is very different from Trapa incisa, and it must not be eaten.'

We see then that the Japanese, like the Chinese, distinguish between *Trapa* and *Trapella*, though at the same time noting the points of resemblance.

Although in the following sections all the appearances presented by the vegetative and reproductive organs of *Trapella* are entered on in more or less detail, special attention is given to certain striking anomalies in structure and development shown in the ovules. Not only are these described in detail, but throughout the account mention of analogous cases—whether in remote or allied types—is introduced for comparison where it would seem that such reference is required.

I introduce here a technical description of the genus, based on that given in the 'Icones Plantarum,' but altered from that in so far as the examination of more complete or better preserved material requires it.

TRAPELLA, Oliv. in Hook. Ic. Plant. tab. 1595. (Char. emend.).

Calyx tubo ovario adnato, limbo libero 5-fido, lobis ovatis acutis. Corolla perigyna tubuloso-infundibuliformis, limbo

¹ T. incisa is given as a variety of T. bispinosa by C. B. Clarke in Hook. Flor. Brit. Ind. Vol. ii. p. 290.

patente bilabiato albido v. pallide caerulescente. labio superiore breviter bifido lobulis rotundatis, labio inferiore trifido lobulis rotundatis, centrali paulo minore; tubo flavido basi abrupte angustato; aestivatione imbricata, labio superiore exteriore. Stamina pollinifera 2 epipetala inclusa, antheris bilocularibus loculis sub-parallelis v. leviter divergentibus connectivo peltato rotundato carnosulo insidentibus: filamentis filiformibus olabris; staminodia antica 2 elongata, antheris rudimentariis: stamen posticum o. Ovarium inferum apice tantum liberum biloculare, loculo antico rudimentario, loculo postico bi-ovulato; stylo gracile elongato, stigmate basi lateraliter dilatato bilabiato lobo postico minore adnato; ovula 2, anatropa prope apicem cavitatis septo inserta pendula, superiore sessili, inferiore breviter funiculato deinde abortivo. Fructus angustus elongatus monospermus indehiscens, apice appendicibus 5 coronatus 3 elongatis rigidis gracilibus arrectis apice uncinatim incurvis, 2 brevioribus spinosis anguste subulatis rectis patentibus; pericarpio tenuiter chartaceo-lignoso. Semen pendulum, elongatum, cylindraceum, endospermio tenui; embryonis recti radicula supera, cotvledonibus linearioblongis semi-teretibus radicula brevioribus.—Herba natans, foliis oppositis petiolatis, inferioribus lineari-oblongis basi angustatis denticulatis, superioribus deltoideo-rotundatis v. cordiformibus obtusis crenato-denticulatis glabratis v. nervis subtus puberulis. Flores axillares, solitarii, pedunculati; pedunculus fructiferus recurvus.

T. SINENSIS, Oliv. l. c. (sp. unica). HAB. Ichang, China, Dr. A. Henry.

Caulis gracilis inferne radices fibrosas ad nodos emittens. Folia superiora 25–30 mm. lata; petiolus 15–20 mm. longus, inferiora 30–50 mm. longa, 5–7 mm. lata. Flores pedunculati, pedunculus 12–25 mm. longus; corolla perigyna 10–15 mm. longa. Fructus 15–20 mm. longus, 2–3 mm. latus; spinis apicalibus longioribus 40–70 mm. longis, 2 brevioribus 3–5 mm. longis.

THE FLOWERS.

These are borne solitary in the leaf-axils, one only as a rule being developed at each node. Those which reach the surface open normally, but many—found especially in the axils of the submerged leaves, occasionally also in those of floating ones—remain quite small and closed. These are the cleistogamic flowers, to be described hereafter.

The pedicels reach a length of about 25 mm. and show a slight thickening at their distal end, corresponding to the inferior ovary, which becomes more prominent after the fall Immediately below the calvx-lobes, and of the corolla. alternating with them, are already visible rudiments of the five fruit-spines. These are one anterior (a. s.) and two small posterior tubercles (p.s.), and a minute elevation on either side (l.s.); these are seen in Figs. 10 and 11, which are anterior and posterior views of the ovary at this period. The free part of the calvx is inserted just above them, and is divided into five acute segments, with imbricate aestivation in bud. The outer surface of the calyx, and of the pedicel, is densely covered with 4-rayed epidermal glands (indicated in Fig. 16), similar to those on the leaves described on p. 101. The corolla is infundibuliform with spreading limb; the two posterior lobes forming the upper, the three anterior the lower lip. The anterior median lobe (a.p. Figs. 3, 4, 5) is inside in aestivation, the two posterior (p, p) outside, and the two lateral lobes (l.p.) half inside, half outside. The tube and lobes show a beautiful pencilling well rendered in the Figures.

The curious stamens are inserted in the corolla-tube (Fig. 5) and are visible at its mouth, though not projecting. The posterior pair (s. m.) alone are fertile, and their structure is interesting enough to be described. The connective has the form of a flat circular disc, attached to the filament in a peltate manner (Figs. 6 a and b are front and back views of a single stamen), the anther-cells being inserted at its upper edge, a trifle to the outer side of the median line. The cells are slightly divergent, with longitudinal dehiscence. In Fig. 23

is given a transverse section corresponding to A-B in Fig. 6b, showing the anther after dehiscence.

The anterior pair are barren and to be regarded as stami-

nodes. The connective is here smaller than in the fertile stamens, but still peltate. Its upper edge is drawn out into two small pegs, to each of which is attached a small barren anther-cell (Figs. 7a and b). These are slightly divergent, as in the stamens; evidently the staminodes have been derived from a pair of stamens quite like the fertile ones here.

Of the median posterior stamen no trace remains.



FIG. 7.—FLORAL DIAGRAM.

The stamens in Pedalineae vary considerably from one genus to another. Thus in *Pretrea* I find the anthers parallel and dorsifixed, with no conspicuous development of connective; in *Pedalium* the anthers are divergent, and the connective produced into a small glandular apiculus; the same holds for *Harpagophytum*.

On removing the corolla and cutting away the calyx-limb, the free part of the ovary is seen, terminating in the style, inserted somewhat anteriorly. The stigma is interesting, being cruciform; in this it deviates from the ordinary Pedalinaceous structure which is bi-lamellate, i.e. with equal anterior and posterior lobes. The cruciform stigma of *Trapella* is doubtless derived from this type. The cross-like form is due to horizontal lobes standing out right and left (see Figs. 8 and 9) at the insertion of the anterior and posterior lamellae. These lamellae are not equally developed, but the posterior has undergone great reduction² (Fig. 9 gives

¹ See my paper, 'Ueb. Fortleitung d. Reizes bei reizbaren Narben,' in Ber. d. deut. bot. Ges. 1887.

² It is to be noted that although the *anterior* loculus of the ovary is almost obsolete, it is the *posterior* stigmatic lobe which has undergone reduction. This is

posterior aspect), so that the anterior lamella towers above it. A longitudinal median section shows the exact relations of the lamellae (Fig. 22). The surfaces, corresponding to the inner applied faces of an unmodified stigma, are covered with stigmatic hairs—the posterior, reduced lobe (p.l.) having its papillose surface continued some little distance down its posterior face (see Fig. 22). The two vascular bundles, running respectively dorsally and ventrally in the style, die out at the base of the stigmatic lobes.

Passing on to the ovary itself, I have been able to show that this is in reality two-celled; but from the fact of one of these cells—the anterior—being quite rudimentary, it escaped notice in the original diagnosis made from imperfect material. The placentation is axile, and the two ovules are inserted high up in the free part of the ovary. These are shown in situ in Fig. 18; here we have represented the upper part of the ovary after the removal of the right side. Both are pendulous, and apparently anatropous, with superior (and exterior) micropyle. They are attached, right and left of the median line, to the top of the partition separating the reduced and fully-developed loculi. The upper (ov.1) attached on the right side of the median line is sessile, but the lower one $(ov.^2)$ is suspended by a longish funicle (fun.). The point of insertion of the funicle is slightly below that of the sessile ovule (ov.1), and to the left of the median line. In Figs. 19 and 20 are given longitudinal sections through the insertion of the ovules ov.1 and ov.2 respectively; Fig. 19 being slightly to the right and Fig. 20 to the left of the absolutely median section.

The rudimentary loculus (red. l.) is on the anterior side of the partition, and there is projecting into it, near the top, a small cushion of tissue (r Figs. 18 and 21), representing perhaps a rudimentary ovule.

especially well seen in a median antero-posterior section of a cleistogamic flower (Fig. 21), in which the stigma is sessile on the ovary. This would point to the fact that entirely different factors have been at work in causing the reduction in the two cases, and that we have not to deal simply with the gradual atrophy of one or other carpel, as might at first be supposed.

The relations of the parts may be elucidated by the examination of a number of transverse sections, taken through the flower at different heights. Such a series is given in Figs. 40-45. In these sections the vascular bundles running to the different floral organs are variously coloured. Those to the carpels are blue, to the stamens yellow, red to the petals, and green to the calyx-lobes. Fig. 40 is a transverse section cut half-way down the ovary. The rudimentary anterior loculus (red. l.) is a mere slit in the thick wall of the ovary, co-extensive however with the fully-developed (posterior) loculus (loc.). The position which should be occupied by the vascular bundle to the posterior stamen which has become obsolete—is indicated by a x. Of the four bundles (blue) belonging to the carpels, the anterior and posterior ones are continued unbranched to the top of the ovary, and up the style (cf. Figs. 40-45).

The other pair, lying right and left in the partition, supply the two ovules, the right-hand one the sessile $(ov.^1)$, the left-hand one the stalked ovule $(ov.^2)$.

Fig. 41 is cut just at the insertion of the spines. Five new bundles, tinted brown, are seen, outside and opposite the red ones of the corolla; these run into the five spines, and are inserted on those which pass up to the corolla.

In Fig. 42 the section passes through the base of the free part of the ovary, the calyx-tube being seen on the outside free from it. Corolla and stamens are not drawn, having fallen away. Fig. 43, higher up still, shows the insertion of the lower stalked ovule and the bundle passing to it; Fig. 44 that of the upper sessile ovule. The bundle to this ovule is seen cut across twice—due to its arching over before running to the ovule (cf. also Figs. 19 and 20). In Fig. 43 is seen projecting into the anterior reduced loculus the small cellular cushion (r), which may be possibly an ovule-rudiment. Later it becomes tightly pressed against the outer wall of the ovary, and possibly assists in the transfer of nutriment from the ovary-wall to the ripening ovule. A longitudinal section through this rudiment is

given in Fig. 39. Finally, the section in Fig. 45 is across the style.

It is the upper sessile ovule $(ov.^1)$ alone in which development is continued after fertilization; the lower one $(ov.^2)$, though up to the stage of fertilization it in no way differs from the upper, except in the possession of a funicle and in being slightly smaller, ceases to grow. With care it may be found, even in an old fruit, as a collapsed remnant, near to the point of attachment of the seed. In the upper ovule $(ov.^1)$ development after fertilization appears to be very rapid; it grows down extending towards the base of the loculus, which it ultimately completely fills (Fig. 35). The details of this development will be resumed directly.

Development of the fruit-appendages.—At the time of flowering the rudiments of the spines are visible, and before the corolla has fallen away, have quite a tangible presence. In Figs. 10 and 11 these rudiments are shown; 10 is the anterior face and shows an unpaired rudiment (a.s.) situated below the interval between the two anterior sepals. In 11 are shown the paired rudiments (p.s.) of the posterior spines, and in both figures, the less conspicuous paired rudiments of the lateral spines are represented (l.s.).

After the fall of the corolla the calyx-lobes close over the ovary, and remain with their edges overlapping. The five rudiments grow out into spines, as indicated in Figs. 12, 13 and 14. The last number represents the mature fruit. The paired lateral appendages (l.s.) alone remain comparatively short, each rigid and sharply pointed. The anterior and posterior spines grow out to a great length—often exceeding that of both fruit and pedicel. As the fruit ripens, their ends become incurved in a circinate manner (Fig. 14), and the whole fruit—both pericarp and spines—becomes much hardened and lignified. As the fruits ripen their pedicels usually become recurved, as shown in Fig. 1, and the fruits are in this way brought down to or even slightly below the surface of the water. In the ripe fruit the pedicel becomes extremely brittle at the point of its insertion in the

leaf-axil, so that if the fruit be disturbed in any way it breaks off. The fruits offer every opportunity for distribution, with their clinging, coiled appendages, and it is surprising that our plant has so circumscribed a distribution, contrary to what is usual amongst aquatics apparently by no means so well-furnished as *Trapella*.

Cleistogamic flowers.—The examination of several complete specimens of Trapella does not fail to show not only the presence of fruits in the axils of the floating, but also sometimes in those of the submerged leaves which can never have been exposed to the air. This at once suggests the presence of cleistogamic¹, in addition to normal flowers, as indeed proves to be the case. Careful investigation of the leaf-axils demonstrates the presence of minute unopened flowers about 2-3 mm. in length, in the axils of many of the submerged leaves. These are cleistogamic flowers, and are at no time open. The calyx remains tightly folded over them and the corolla is reduced, and, so far as I could ascertain, two fertile anthers are developed, but in most cases these parts were disorganised. The stigma is here sessile on the top of the ovary (Fig. 21); in this lies their chief structural difference from normal flowers. The pollen is applied directly on to the stigma from the anthers. The cells of the ovary, insertion and number of ovules, &c., are quite similar in both forms, as also is their further history after fertilisation. Hence in order to distinguish whether any fruit has been cleistogamically or normally produced it must be noted, (1) whether it comes from the axil of a submerged or floating leaf; (2) whether it is pedicellate or almost sessile; (3) whether its stigma is sessile on the top of the ovary or not. No. I is not however absolute, as I have not unfrequently found cleistogamic flowers in the axils of floating leaves, even of

¹ Cleistogamic flowers are well known in many aquatic plants: Darwin mentions (Forms of Flowers) instances in Ranunculus aquatilis, Alisma natans, Subularia aquatica, Illecebrum verticillatum, Menyanthes, Euryale and Hottonia inflata (Torrey in Bull. Torrey Botan. Club, vol. ii. p. 22). In none of these would there appear to be any modification of structure, other than a mere reduction of parts due to their remaining closed.

leaves nearer to the growing-point than fruits which have been normally developed. The cleistogamic flowers are simply slightly arrested normal ones, and their presence on the floating parts is perhaps due to the fact that, for some reason, it was difficult for them to reach the surface. It would be interesting to investigate whether cleistogamic flowers cannot be produced at will in *Trapella*, an experiment which might easily be performed—should the plant come into cultivation—by artificially keeping the flower-buds below the surface of the water. It seems quite probable that in this way cleistogamic flowers would be produced, and these in considerable numbers, showing that they are interchangeable, and that the production, in any case, of one form or the other depends on external causes rather than on any internal tendency.

Mature fruits, in whichever way produced, are similarly appendaged. They are naturally held at the level of the water or at a depth of some 3 or 4—or if cleistogamic of, at the most, 8—10 cm. Fish occur to me as the most probable agents in dispersal here, and the incurved fruit-appendages are admirably adapted to clinging to their spines. Jäggi¹ has suggested that fish are instrumental in distributing the somewhat similarly appendaged fruits of *Trapa natans*; but both Ascherson² and Nathorst³ give it as their opinion, that more probably it is by ducks or other aquatic birds. In *Trapella* we have the same conditions to deal with, and a much greater proneness of the fruits to become entangled; it is on this account a great puzzle to me that this plant should have so circumscribed a distribution⁴. Still it may

¹ J. Jäggi, Die Wassernuss, Trapa natans, L., 1883.

Ascherson, in Bot. Centralbl. Bd. xvii. p. 248.
 Nathorst, in Bot. Centralbl. Bd. xviii. p. 278.

⁴ Dr. Henry states that he only found *Trapella* in *one* pond out of some twenty he had seen. The pond in question differed from the others, he says, in being on the top of a hill, so that the water was little affected by floods of rain; nor was the pond used for irrigation purposes, so that its undisturbed condition would be especially favourable to our plant, and might account for this being its sole habitat in the district. In the event of *fish* being the agents in question, distribution would depend on the facilities for their visiting other ponds.

be that when this little known region is more thoroughly worked out, *Trapella* may turn out to be a fairly common plant.

Development of the flower.—In the youngest buds that I have been able to investigate, all the organs were already formed. Fig. 16 is an antero-posterior section of a bud less than 1 mm. long. In it are seen the functional and reduced loculi of the ovary (loc. and red. l. respectively), and the insertion of the upper sessile ovule (ov.1). The lower ovule-which originated side by side with the upper-fills up the rest of the cavity of the ovary, but is not represented in the figure, since its point of insertion cannot be given. In Fig. 17 is the section at right angles to the antero-posterior plane, showing the insertion of the stamens and the state of pollen-development. As yet the pollen-mother-cells (p, m, c.) are undivided, and lie enclosed in the tapetal layer (tap.). At this stage about equal parts of the ovary are inferior and free respectively, and the vascular bundles, drawn darker, show some differentiation, though of course they are not lignified as the parts have still to undergo great stretching. Gradually the lower part of the ovary elongates, leaving the ovules high up, attached to the axile placenta quite at the top (Fig. 15): then later on, after fertilization, the uppermost ovule comes almost to fill this deep ovary.

Development of ovule and embryo-sac.—Up to a certain point the developmental history of both upper and lower ovules is identical; since, however, in all cases it is the upper one only which becomes a seed, it will be the history of this one which I shall follow, except where otherwise indicated.

The ovule is essentially anatropous from a very early stage (Fig. 24). The nucellus is small in comparison with its developing integument (ct). In stages a trifle earlier than the one figured, the undivided archesporial cell may be seen, occupying the upper part of the nucellus, and invested only by a single epidermal layer. In Fig. 24 the archesporium has divided into two cells: an upper one (e. s. m. c.), which is the embryo-sac mother-cell, and a lower one (c), which later will

give rise to two cells, one above the other. The very thick integument now closes over the free end of the nucellus. There is, as is customary in Monopetalae, only one integument formed. The closure of the integument is very complete, and the micropyle is reduced to a mere line (*m* in Fig. 27). Indeed in some cases I could detect no trace of this even (as in Fig. 26), and without proper developmental stages, the ovule might easily have been judged to be a naked one.

The cell which is cut off from the archesporal cell lies, not, be it noted, as is usual, at the micropylar, but at the opposite end of the embryo-sac mother-cell. This first cell (c in Fig. 24) is sister-cell to the embryo-sac mother-cell, and divides by a horizontal wall into two cap-cells (c^2 and c^3 in Figs. 25–28). The embryo-sac mother-cell itself also divides, and a new cap-cell (c^1 in Figs. 25–28) is cut off, lying between the embryo-sac and the two lower cap-cells. There is now a row of four cells, the uppermost of which is the embryo-sac (as in Fig. 25). In one case only did I find an exception to this state of things. In this, not the top, but the second cell of the row, became the embryo-sac; it thus had one cap-cell above and two below it.

By the succeeding growth of the ovule, the embryo-sac comes to lie very deeply, approaching very nearly the lower-most tip of the ovule (Fig. 19). No *raphe* whatever is developed; the vascular bundle ends abruptly at the insertion of the ovule (Figs. 19, 31, 32, 36). There can, however, be no doubt as to the base of the embryo-sac being, theoretically, the chalazal end.

In early flowering stages are found, the three cap-cells $(c^1, c^2, c^3, \text{ Fig. 25})$ of fairly equal height, and the embryo-sac, above, fairly rectangular in form; in slightly older stages the topmost (Fig. 26) of the three cap-cells (c^1) becomes partially absorbed, and then the second of them $(c^2, \text{ Fig. 27})$. The terminal cell (c^3) always increases in length, at first at the expense of c^1 and c^2 . The walls of the embryo-sac and of these cap-cells are highly refringent and deliquescent, as is usually the case. In each cap-cell is a large, round nucleus.

At the time when the two proximal cap-cells $(c^1 \text{ and } c^2)$ begin to dwindle, the embryo-sac goes through the stages which precede fertilization. The single nucleus of the embryo-sac divides into two (Fig. 27), and each of these gives rise in the normal manner to the egg-apparatus, antipodals, &c. In Fig. 28 the embryo-sac is ready for fertilization. Its upper (micropylar) end has become much widened and its apex pointed. A line (m) representing the micropyle is seen in Fig. 27, and in Fig. 28 this is occupied by the pollen-tube (p. t.) The nuclei constituting the group of antipodals (ant.) are of small account and shortly dwindle.

It must be observed that in this stage the tip of the apical cap-cell (c^3) has become pointed, and that it gradually elongates downwards. A later stage is given in Fig. 29: this however is taken from the *lower* ovule. The apical cap-cell here almost equals the embryo-sac in length. In the embryo-sac itself I have only drawn one nucleus, as the others were not distinguishable. The stage is given to help to fill a gap in the history of the upper ovule. It seems, however, certain that this cap-cell steadily elongates.

From this point the lower ovule gradually retrogrades, and hangs, in older stages, as a shrivelled remnant, which may be found with care even in ripe fruits, as already noted.

The upper ovule now begins to elongate very rapidly so as to extend right down into the lower region of the loculus. That active division of the cells of the nucellus and integument is taking place may be seen from the arrangement in rows of the flat cells on either side of the embryo-sac in Figures 26, 27. The stage next following, in which the egg-cell undergoes its first segmentation and endosperm begins to form, I have not been fortunate enough to secure. My youngest fruit, though younger than that given in Fig. 12, where the spines are just showing prominently, has a much elongated ovule, in which profound changes have already occurred. The changes must be very rapidly passed through at this point, since in the material at hand I have been able to obtain numerous preparations of the stages both before and after the hiatus

in question. I hope at some future time to be able to fill it up.

After fertilization.—Passing on now to the next oldest stage found, which is given in Fig. 30. The ovule has elongated much and continues to do so until the ripening of the seed, when it entirely fills the loculus (Fig. 35). In Fig. 30 the fertilized egg-cell has already divided and a long suspensor formed (sp.); the latter remains attached to one side of the embryo-sac very near its upper end, and by its elongation the embryonic cell (emb.), in which no divisions have yet arisen, is carried to a point below the middle of the embryo-sac. The contents of the embryo-sac (other than the embryo and suspensor) are shaded in the figure. A development of endosperm has taken place, but is confined to the lower two-thirds of the embryo-sac; in the synergidal region no cell-division takes place.

At the base of the embryo-sac a most unusual appearance is seen. The lowest cap-cell (c^3), as above described, was found to elongate very much; now it has considerably outstripped the embryo-sac in length; further, by a longitudinal median wall it has become divided into symmetrical halves. 'appendage,' as I shall at present denote this structure, consists therefore of two very long, tapering cells, applied side to side and ensheathed in the down-growing ovular tissue. The walls of this appendage are brightly shining and fairly thick, and consist of unaltered cellulose. Its contents are richly protoplasmic, and each of its cells contains near its proximal end a large nucleus (n). At this time, and in the next following stages, the appendage contains great quantities of small starch-granules, no doubt transitory. This extraordinary structure is, I believe, to be regarded as an absorptive organ. By its large surface much food-material is absorbed from the tissues outside it (perisperm), which is in turn passed on to the embryo-sac; the embryo-sac from this point increasing in bulk at the expense of the outside tissues. So long as this continues do we find transitory starch-granules deposited in the appendage. In later stages—when its object is fulfilled—the appendage is found with sparing, highly vacuolated protoplasm, and with nuclei much lobed, and showing a tendency to fragmentation (Figs. 34, 34 a). As the ripening seed and embryosac increase in size, the appendage becomes relatively less important, as in Fig. 32, and especially in Fig. 35, where it is but an appendix to the ripe seed.

In favourable preparations, what I take to be the dwindled remains of the two proximal cap-cells (Fig. 33, c^1 and c^2) may still be made out. These flattened remnants in older stages are not to be found. These dwindling cap-cells retain still their deliquescent walls—in contradistinction to those of the endosperm. In later stages, also, the basal parts of the appendage become, to a certain extent, sheathed by a layer of endosperm-cells—as it were a lip growing over it (Fig. 34). This arises only later on, and is perhaps due to the still active elongation of the endosperm, after the tip of the appendage has reached its furthermost limit. Figure 34, showing this, is taken from a section at right angles to Fig. 33. In it the appendage appears to consist of a single cell, an appearance due to the partition-wall being parallel to the plane of the section. This sheathing by endosperm-cells is not generally equal on all sides, but unequal as in Fig. 34.

This appendage—unparalleled so far as I know—is all of a part with the sequence of events in this strange plant. For here is a plant, no doubt descended from forms with superior ovary, in which the only ovule which continues to develop, for some reason elongates downwards with great rapidity, and has in course of time brought about the considerable invagination of the ovary to accommodate it. It is not wonderful then that the plant has, pari passu, seized on a means for supplying its developing endosperm, and ultimately of course the embryo, with food-material. It has been the apical cap-cell, which normally dwindling to nothing, in Trapella has become modified into this embryonic absorptive organ.

As the seed ripens it is to be noticed that the wall of that part of the ovary which is above the insertion of the calyx-limb, and which before fertilization was thick and very

succulent, and the cells of which were richly starch-containing, becomes quite shrivelled, from the travelling away of these stores, which are conveyed to the developing seed.

Resuming the history of the embryo-sac and its contents. As the endosperm continues to grow, it gradually encroaches on the tissues lying outside it. Indeed the process is continued until of the nucellus and integument we have remaining, throughout the greater part of the seed, only a single layer of cells (int., Fig. 37).

As already stated for the earlier stages, no endosperm formation takes place in the micropylar region of the embryosac. This region is occupied by the synergidae, and perhaps a certain amount of protoplasmic remainder; these, instead of dwindling after fertilization in the usual manner, go on increasing much in bulk. By the time that the seed is ripe, so large have they become that there is a conspicuous tubercle which I shall speak of as the synergidal tubercle—present at the top of the seed (Figs. 35 and 37). It is the side of this tubercle which is attached to the placenta, and, externally, it is separated from the rest of the seed by conspicuous constriction. In such a stage as that represented in Figure 36 these greatly developed synergidae have a granular protoplasm. often highly vacuolated; each synergida containing a large nucleus (n.) with tendency to fragmentation. In the ripe seed they have reached their maximum development, and their protoplasm shows a very curious, congealed-looking reticulum. Immediately round the edge there is a denser limiting layer, but the bulk is made up of the oddly areolated, granular and sometimes vacuolated protoplasm. It is difficult to describe the effect in question, but in Fig. 38 I have given an enlarged view of the region around A in Figure 37, which comes as near to the appearance in question as I can manage. The large, lobed, fragmenting nuclei present a very degenerated appearance, coloured often a deep brown or black by tannin. Each is surrounded by a small, comparatively homogeneous, protoplasmic areola (n.a.), which does not show the typical reticulations of the other regions.

As the endosperm is developing, we find that its upper layers have their cells arranged in strata, more or less parallel to the base of the synergidal region (l. d. Fig. 36). The cells making up the layers in question are large and conspicuously granular, with large, well-defined nuclei; and in later stages their walls become thickened and lignified. In this way a diaphragm is formed across the embryo-sac, absolutely cutting off the synergidal region from that which is occupied by the endosperm and embryo.

In Fig. 36 are seen the preparations for this diaphragm, i.e. the parallel rows of cells, l.d.: in Figs. 37 and 38 the walls of these cells constituting the diaphragm have become lignified and are drawn in black (l.d.). The transition from the lignified diaphragm to the non-lignified normal endosperm below it is as sudden as it is represented as being in the figures. At the most, the diaphragm is five or six layers deep.

We find in the adult seed that its narrowest part corresponds to this diaphragm (Fig. 35 and 37). This is due to the fact that the other parts go on expanding (corresponding to the growth of the embryo &c.) after the diaphragm has become hardened and non-extensible; hence in this region a circular constriction is formed. The development of such a barrier is, doubtless, to prevent any contamination of the embryo and endosperm in which it lies, by the death and possible subsequent decay of the synergidae.

It may be that these enlarged synergidae in some way assist in the absorption of food-material from the placenta just as the appendage at the other end does from the tissues of the nucellus and integument. Indeed the occurrence of such a sucker at one end of the embryo-sac does not render it at all less probable that there will be one at the other. It is interesting to compare the respective morphological values of the two special organs in question, in the one case a cap-cell, in the other the synergidae, and to notice how by a special adaptation they play, on this view, identical rôles.

The embryo, meanwhile, has been developing. In Figure 30 the suspensor has elongated, and the embryonic cell has been carried down and become immersed in the endosperm. There is no point of special interest in its mode of segmenta-The developing embryo gradually encroaches upon the endosperm, which it absorbs. Soon after the stage represented in Fig. 36, the two cotyledons are differentiated (Fig. 46) and the arrangement of tissues at the root-apex is that obtaining in the adult root. The root end is gradually brought higher up towards the micropylar end of the embryosac (Fig. 27), and the shoot end (with the cotyledons), to the base of the seed, so that ultimately only a narrow layer of endosperm remains between the cotyledons and the appendage (Fig. 35). In Figure 47, the arrangement of the tissues of the young root-apex is well shown. This apex is from an embryo of about the same age as Fig. 46. There is an independent plerome (pl.), and a periblem (pb.) arising from a single layer of cells. Outside, and independent of this, is the dermato-calyptrogenic layer (d.c.). At the apex the suspensor (sp.) is attached. Essentially the same arrangement is retained in the ripe seed (Fig. 37), though here the tip of the radicle is very much wider, and the number of cells formed from the three initial groups much greater.

In the ripe seed there is a considerable width of endosperm remaining (some six or eight layers), the cells of which are stored with aleurone-grains and oil-droplets. It is not surprising that the seed was originally described as being 'exalbuminous,' for the tissues of the integument are, in the ripe seed, reduced to a single layer of cells (=testa), so that without embryological evidence it would be impossible to regard what I find to be endosperm, as other than integument. In *Pedalium* even—usually described as exalbuminous—I find also several layers of true endosperm, almost as much as in *Trapella*.

With the ripening of the seed the suspensor is gradually obliterated; the walls of that part which runs through the synergidal tubercle become pressed together, so that only

here and there is its lumen visible (Fig. 37, \mathfrak{sp} .). That part which runs through the 'diaphragm' is early lost to view—though in Fig. 36, where the diaphragm is not yet lignified, the whole course of the suspensor can be traced. Finally, its lowest segment, which abuts upon the embryo, is lost with the elongating of the radicle—all that remains being some three or four cells attached to the apex of the radicle, and flattened, more or less, up against it (Fig. 37, \mathfrak{sp}^1 .).

Before passing on to describe the vegetative organs of *Trapella*, it will be well to see in how far the conditions I have just described are to be regarded as unique. Our plant combines in itself so many unusual characters, any one of which would make it remarkable, that such a digression may be justified.

The early stages of development of the ovule forcibly recall similar conditions in *Hippuris*. At a very early stage the nucellus becomes invested in the ample single integument, and in it, as in Trapella, it becomes difficult to decide (older stages only being examined) whether the ovule is naked or not. Unger¹, Schacht², and Schleiden³ all describe the ovule of Hippuris as being destitute of integument, and it is only recently that Fischer 4 has explained what really takes place. The embryo-sac mother-cell in Hippuris gives rise by transverse divisions to a row of four sister cells; the three upper ones become quickly absorbed,—the nucellus—with the gradually enlarging embryo-sac-becomes enveloped in the developing integument. The behaviour of the epidermal cell lying at the top of the nucellus is peculiar; it undergoes a longitudinal division, and then both cells undergo a number of transverse divisions, so that a small wedge-shaped cushion of cells is formed at the micropylar apex of the embryo-sac. The cushion plays the part of preventing the micropyle from

¹ F. Unger, Die Entwicklung d. Embryo's von Hippuris vulgaris, in Bot. Ztg. 1849, p. 329.

² H. Schacht, Entwicklungsgesch. d. Pflanzen-Embryon., Tab. xxv. fig. 12. ³ Schleiden, Nova acta Acad. Leop. carol., vol. xix. Tab. v. fig. 69.

⁴ A. Fischer, Zur Kennt. d. Embryosackentwicklung, &c., in Jenaische Zeitschrift, Bd. xix (1880), pp. 117-120.

being entirely closed by the powerfully developed integument (loc. cit. p. 119), and allows the embryo-sac as it elongates to make its way some little distance up the micropyle—the cushion of cells being driven like a root-cap in front of it. In Trapella such an apical cushion is not developed, which perhaps accounts for the difficulty in recognising the micropyle in any but the youngest stages.

Fischer points out (loc. cit. p. 120) how Hippuris displays monopetalous characters in the development of its ovule. Besides being similar to Trapella in these, it seems that a considerable space at the top of the embryo-sac in Hippuris is left unoccupied by endosperm1. This region does not enlarge or form the well-marked tubercle found in Trapella. but we see in Hippuris 2 a state of things which may have existed in the group of plants from which our type has sprung. In many Monopetalae, indeed, considerable space is left, in the synergidal region, unoccupied by endosperm; and in several genera, Lathraea, Pedicularis, Lamium, Veronica, &c., there arise from this upper region appendages and caeca of an extraordinary nature; these make their way in amongst the tissues of the ovule. It would seem that when the synergidal region is left unoccupied in this way, there is a proneness to singular developments of one sort or another.

In *Trapella* the cap-cells normally all lie below, i. e. at the chalazal end of, the embryo-sac, and not at its micropylar end. It is the *uppermost* cell of the row which becomes the embryo-sac³. This state of things is only paralleled, to my knowledge, in *Rosa livida*, described by Strasburger⁴ and A. Fischer⁵. In this plant Strasburger found often the second

1 Vide figures to Unger's paper, in Bot. Ztg. 1849.

⁴ Strasburger, Angiospermen und Gymnospermen, pp. 15-16.

² As will be shown later, the vascular cylinder in the stem of *Trapella* much resembles that in *Hippuris*.

³ In one ovule of *Trapella* only, I found that the second cell of the row became the embryo-sac.

⁵ A. Fischer, Zur Kenntn. d. Embryosackentwicklung, &c., in Jenaische Zeitschrift, Bd. xix (1880), p. 120.

In Atherurus attenuatus (Aroideae) as figured by B. Jönsson [Om embryosäckens utvecklung hos Angiosperna, Tab. viii. fig. 12, in Lund's Universitets Ärs-

or third cell of the row developed into the embryo-sac, the other daughter-cells being ultimately absorbed. Fischer, who investigated several other genera of Rosaceae, failed to find this behaviour in any other case.

In Loranthus sphaerocarpus, from Treub's ¹ account, it seems that each embryo-sac mother-cell divides into a row of three, of which the top one in each row becomes the embryo-sac, increasing in length. The two small cap-cells below (anticlines of Treub) disappear, and the narrow embryo-sac elongates downwards very much, penetrating with its pointed tip the tissues to a considerable depth. Here then is a case analogous to that of Trapella.

In a few plants the antipodal cells at the base of the embryo-sac are conspicuously developed. Thus Hofmeister² gives in his figures several cases of this, though usually they are hardly commented upon in the text. In Asarum europaeum and canadense the embryo-sac is long and narrow, and the three antipodals are very long, extending, at fertilization, from one third to one half up the embryo-sac. Thus they remain, or may divide up forming a small tissue. Jönsson³ also examined this genus, but in his figures the antipodals are not proportionally so long as Hofmeister gives them. In Crocus vernus the embryo-sac is very broad, and the antipodals, though not relatively very large, form a prominent beak at the centre of the base of the embryo-sac. They disappear later.

In no case do we meet with a persistent, enlarged cap-cell as in *Trapella*. The antipodals of *Asarum*, as figured by Hofmeister, are the only structures at all recalling it, but differ morphologically. In *Loranthus sphaerocarpus* the lower

skrift, T. xvi (1880)] it is the second cell of the row of daughter-cells which becomes the embryo-sac. I am unable to read this interesting, but somewhat inaccessible paper, it being in Swedish.

¹ M. Treub, Obs. sur les Loranthacées, in Annales du Jardin botanique de Buitenzorg. T. ii (1881), p. 54.

² W. Hofmeister, Neue Beiträge z. Kennt. d. Embryobildung d. Phanerogamen, Tab. x. fig 12, in Abh. d. K. S. Ges. d. Wiss. vi. 1859.

³ loc cit., Tab. viii. fig. 7.

end of the embryo-sac elongates, penetrating the tissues, but neither is there any homology here.

It is interesting to remember that amongst the few plants in which it is stated no endosperm is at any time formed, Hofmeister gives *Trapa* as one (also *Zostera*, *Naias*, *Tropaeolum*, and Orchidaceae).

ANATOMY OF VEGETATIVE ORGANS.

The Stem.—In Trapella the stem has an average thickness of 1.5 mm., and conforms in its general structure to the normal, reduced, aquatic type. It consists of an axial vascular cylinder, surrounded by a wide parenchymatous cortex freely supplied with air-spaces. In different regions of the stem these spaces differ in their extent. No peripheral bundles whatever are present, and the vascular cylinder—which runs unbranched throughout the internodes—is delimited by a very well-marked endodermis (cns., Figs. 49–51). In the adult parts of the stem, the radial walls of the endodermis are thickened in a very characteristic manner (Fig. 51).

In the axial bundle-cylinder, and immediately surrounding a central 'pith,' is a ring of vessels, constituting the xylem (vv., Fig. 51), which, in its distribution, recalls that of Hippuris vulgaris. Outside this is a zone of thin-walled tissue, which is the phloem, and consists, for the most part, of sieve-tubes. Externally this zone is limited by a well-marked endodermis (ens., Fig. 51). The 'pith' consists of thin-walled parenchymacells, oblong in longitudinal section, and with longitudinal axes about three times as great as the transverse. They contain a number of small starch-granules. Here and there, in the pith, an intercellular space (i.s., Fig. 51) is seen, due to the breaking down of spiral vessels; in them, at places, the remains of the spiral coil may be seen remaining. The vessels are both spiral and scalariform; in the former case the spire is a close one. The cells which immediately abut on the outside of the ring of vessels are wide and resemble those of the pith.

Next follows a zone of sieve-tubes, with a width varying from two to three tubes. Sieve-plates occur only upon the

horizontal walls, separating the different members of any tube. Each horizontal wall constitutes a single sieve-plate, both faces of which are callous, as shown by appropriate re-agents (corallin-soda, &c.). The outermost sieve-tubes of the zone have a narrower lumen than the other ones, and are generally (in my material, gathered, July) found obliterated by callusplates (c.p., Fig. 56). The inner ones, though also callous, are not sufficiently so to be obliterated.

In longitudinal section the latter show the familiar schlauch-köpfe (s.k., Fig. 55), with quantities of mucilaginous droplets and granules, in the neighbourhood of the sieve-plate. Very narrow companion-cells, with granular protoplasm and small spindle-shaped nuclei, are seen, co-extensive with the sieve-tube members. Besides companion-cells, other narrow, elongated, parenchymatous elements are present, distributed throughout the zone of phloëm. The layer also lying immediately within the endodermis belongs to the same category. It is from this layer—together with the endodermis to a subordinate degree—that the adventitious roots take their origin. The sieve-tubes 1 vary in width from 016-008 mm.; from each sieve-tube member not more than one companion-cell is formed.

The broad cortex is traversed longitudinally by large airspaces. These, in the submerged parts of the stem, are very large (as seen in a transverse section of the stem), extending from the axial cylinder almost to the periphery; there is however usually an outer zone of much smaller spaces (Fig. 50). In the floating regions these spaces are divided up, so that several will lie on any radius. The arrangement indicated will be sufficiently understood by a reference to Fig. 49. These spaces are entirely schizogenetic in their origin.

At the nodes, at which are inserted the floating leaves, a modification of the cortex is met with, of importance

¹ The occurrence of a continuous zone of well-developed sieve-tubes in the reduced vascular cylinder of an aquatic is of interest from their supposed absence in certain cases; v. I. B. Balfour, on the genus *Halophila*, p. 19 in Trans. Bot. Soc. Edinb. 1877–78.

mechanically. Here, in the regions between the leaf-bases (i.e. right and left, supposing the leaves to run anteriorly and posteriorly), the cell-walls of the cortex are strongly thickened, in striking contrast to the thin-walled cortical cells of the internodes. This, no doubt, is to resist the pressure and strain occasioned by the continuous rippling of the water against the leaves. Further, there is present in the hypodermal layer of cells a meristem (cb., Fig. 52), by the activity of which fresh cortical cells can be added to lend, if necessary, additional strength. In Fig. 52, a portion of a cortex at a node is given. The thick-walled cells are strongly pitted where they abut upon one another, but this I have not indicated.

It is only at the nodes that the axial bundle-cylinder is branched. Here there is an anastomosis of equivalent elements, and two bundles are given off (one on either side, Fig. 57) to the leaves. The bundle (l. tr.) running to a leaf passes horizontally through the cortex of the stem and divides into three bundles, which lie in the same horizontal plane. This division into three takes place close to the central bundle-cylinder. The three bundles run undivided up the petiole, and have their elements collaterally arranged. Directly the leaf-bundle enters the axial-cylinder it forks, and its elements anastomose with the groups A and B (see Fig. 57). Immediately above or below the point at which the bundles run in, the normal ring of vessels is seen. The bundle which runs to the axillary bud originates from the main leaf-trace bundle just before it divides into three (l. tr.). In the horizontal section, which shows the insertion of the leaf-bundles, adventitious roots may be seen originating (adv. rt.); these are formed from the layer of cells next below the endodermis, and pierce through the They usually lie dormant, however, in the upper floating nodes of the stem.

The Root.—I have in no instance been able to observe the adult primary root; no doubt it is of little importance, being early superseded by numerous adventitious roots. A transverse section of one of these latter shows, as in the stem, a small central cylinder, surrounded by a wide cortex. The axial

cylinder is bounded by a well-marked endodermis (see Figs. 53 and 54). The air-spaces of the cortex are very largely developed, and are formed simply by the separation from one another of radial plates of cells (Fig. 53). Their arrangement recalls that found in the stem of *Myriophyllum*. Several of the radial lamellae of cells are found collapsed, and are drawn simply as lines in Fig. 53.

The arrangement of the bundles in the axial cylinder, though somewhat reduced, is characteristically *tetrarch*. Each xylemgroup is generally reduced to a single vessel (v.). In Fig. 54, however, the right-hand group is more extensive, and is in connection with the large axial vessel. In the four groups of thin-walled tissue (ph.), which alternate with the xylems, sievetubes may be found, similar to those described in the stem, though not so numerous.

The arrangement of the tissues at the apex of an adventitious root sufficiently resembles that given in Figs. 37 and 47, for the embryonic root, to render further description here needless.

The Leaves.—As has been seen, there are essentially two forms of leaf found, the linear-oblong submerged leaves and the deltoid-rotundate floating ones. In some specimens, leaves intermediate in form (Fig. 63 b) are found at the point where the transition from one form to the other occurs. When the leaves are young, and before they are unfolded, their surfaces are densely covered with small four-celled glands. These are formed in greatest numbers on their undersides. After unfolding many drop off, leaving, however, their pedicelswhich are small round cells, easily distinguishable from the other epidermal cells. In Fig. 60 a is given the surface view of the epidermis of the under side of a floating leaf. There are present four-celled glands (gl.), and also their pedicels (gl^1) , where the gland itself has fallen off. There are no stomata. These are only found on the upper surface of the floating leaves, where they are present in great numbers (Fig. 60 st.). The characteristic glands are also present, and are often eight- instead of four-celled (Fig. 60 gl., also Fig. 61). I have sometimes found stomata like that in Fig. 62, especially

near the edges of the leaves. These, from the arrangement of the guard-cells, must remain permanently open.

In Figs. 64 and 65, a surface view and vertical section of one of these four-celled glands is given. In 64 its pedicel (ϕ .) is supposed to be seen through, and is dotted in. In 65 the exact relations of the parts are given. The development-which can be easily traced in young leaves—is simple. A small cell projects from the epidermis, and is divided by a horizontal wall; the lower cell constitutes the pedicel, the upper enlarges and divides cross-wise into four cells. In some cases, especially on the stem and flower-stalks, the cells of the gland grow out to a great length, forming a distinctly quadrifid gland. The possession of these glands is a decidedly Pedalinaceous character—they are formed in great quantities in *Pedalium*, Pretrea, etc. In these latter genera they secrete mucilage in quantities, preventing the plant from drying up. In Fig. 66 a and b are given views of such a gland from Pretrea for comparison with Figs. 64 and 65. The concentric layers within the cuticle swell and break down into great quantities of mucilage when the gland is placed in water. The shaded rod at the inmost angle of each cell represents the collapsed protoplasm of the cell. That Trapella, an aquatic plant, should need special mucilage-glands to prevent its being dried up is improbable. It may be that their presence in our plant is due to the retention of an ancestral character. In any case, the possession of such glands by many genera of Pedalineae is a point worth noting, though in determining affinities it is possible to place too great belief in anatomical characters.

Another very interesting point in the leaf-anatomy of *Trapella* is the possession of water-glands by both floating and submerged leaves. These are situated in the small incisions of the leaf-margin (one in each), as in *Saxifraga crustata*. Fig. 58 is a vertical section through a water-gland in one of the floating leaves. The string of tracheides may be seen ending in a mass of small-celled tissue, the epithem (e) well-marked off from the surrounding mesophyll. Above the water-gland is the water-pore (w.p.). In Fig. 59 this is seen

in surface view; the pore is formed by the separation of a number of cells, which later on all break down (i.e. the ring of cells surrounding the pore), leaving a large hole. The waterglands of the submerged leaves are similar in structure, though not quite so large. Fig. 63 c is a surface view of two teeth of a submerged leaf, showing the water-glands and the vascular bundles running to them. In the glands of the submerged leaves I was never able to find a mere water-pore; there was always a hole, leading from the epithem to the exterior, formed by the breaking down of a number of epidermal cells. This occurrence of water-glands, on the submerged as well as on the floating leaves of *Trapella*, is of interest, but it is not unique, as in *Callitriche* a similar state of things has been described.

The general arrangement of the mesophyll in the two forms of leaves differs. In the floating leaves there are some three layers of palisade-cells towards the upper face, and spongy parenchyma below. Running in the mesophyll are the small vascular bundles with very well-developed parenchymatous sheaths and collaterally arranged elements.

In the submerged leaves no palisade-tissue is present—the mesophyll having a reduced structure.

AFFINITIES.

From the account of the morphology of the plant, it will be seen that some difficulty must attend the reference of *Trapella* to any existing Natural Order. There can however be little doubt of its belonging to the bilabiate Monopetalae, its more than half-inferior ovary, a rare thing in that series, not-withstanding ². The group of the Labiatiflorae contains a number of Orders, many of which are not well-defined. In

v. De Bary, Comp. Anat. Veg. Organs, &c., Eng. ed. p. 53.

² It will I think be acknowledged that *Trapella* must find its allies among the Monopetalae with superior rather than with those with inferior ovaries. In the latter possibility *Caprifoliaceae* is the only group to which it might be technically allied. In the discussion which follows I am assuming it to be allied to plants with superior ovary.

any case the ordinal distinctions in this assemblage are by no means so well marked as in other groups of Dicotyledons. This applies to the small order Pedalineae, to which *Trapella* has been referred; certain genera being included in it, rather from the difficulty of placing them elsewhere, than from any other reason. Professor Oliver, in referring our plant to Pedalineae, did so, not that it agreed with the more normal genera in all points of structure, but rather as an alternative to making it the type of a new Natural Order intermediate between Pedalineae and Myoporineae.

Not only was such a course expedient, but it was also one that is justified by a careful investigation of adequate spirit-material and a renewed study of the morphology of its supposed allies. In the next few pages I shall try to show that *Trapella*—though differing widely from all known Pedalineae—may yet be traced back to the stock from which it may be conceived the true Pedalineae arose.

Before entering on this matter, it will be well to consider what claims *Trapella* may have to be united to certain other Orders of Monopetalae.

Gesneraceae must be considered as one of the possible homes for *Trapella*, since here alone in the Labiatiflorae do we find in addition to superior, also inferior and semi-inferior-ovaried forms. Our plant essentially differs in having a bilocular ovary with axile placentation and two ovules; Gesneraceae, on the other hand, having a unilocular ovary with two parietal placentas and very numerous ovules. The appendaged seeds of such genera as *Aeschynanthus* offer no possible homologies, the appendages in question being mere outgrowths of the testa. Gesneraceae, it must be remembered, belong essentially to the New-World—the tribe of the Cyrtandreae alone (to which several Chinese genera belong) being Old-World. *Trapella*, if it were found necessary to refer it to Gesneraceae, would have its relationship through this latter tribe.

From Scrophulariaceae, *Trapella* differs in its solitary seed, and in the small amount of endosperm which it contains. It

agrees in its axile placentation; but the spines developed on the fruit are a non-scrophularineous character. This Order gives us but few aquatic members, *Limnophila* and *Hydrotriche*, and isolated species of larger genera, none of which however especially recalls *Trapella*.

Bignoniaceae constitute a homogeneous group with their winged seeds, and, furthermore, essentially parietal placentation, *Trapella* deviating in both these particulars.

Trapella has been referred to Pedalineae, since in this Order occur forms with few ovules, and curiously-appendaged, lignified, non-dehiscent fruits. These characters taken together with its opposite leaves, solitary axillary flowers, and its 'quaternary vesicles' and general disposition, confirm such determination. The appendaged fruit forms an especially strong analogical character.

To Myoporineae *Trapella* approaches very nearly in some respects. In the more typical forms of this Order the ovary is bilocular, with two pendulous ovules in each loculus inserted on the partition. The seeds are often long, with only a small amount of endosperm and superior radicle. The leaves however are rarely opposite, and the fruit is unappendaged. Our plant must thus be classed with Pedalineae rather than here.

The affinity between Myoporineae and Pedalineae I believe may turn out to be a nearer one than that indicated in the Genera Plantarum—indeed Lindley (Vegetable Kingdom) places them very close together. I shall revert to this matter subsequently.

In view of the heteromorphous nature of Pedalineae, as it at present stands, and in view of the possibility of its being divided up in the future and its genera relegated to other Orders, it may be well to see to what genus, or group of genera, now included in Pedalineae, our plant seems most nearly allied ¹.

¹ Since the above was written the concluding part of vol. ix. of Baillon's 'Histoire des Plantes' has appeared, containing Scrophulariaceae. Baillon makes Pedalineae (with the exception of the Martyneae, which will doubtless be treated

An examination of the chief genera 1 soon showed me that those forms with bilocular ovary and axile placentation, in which the loculi do not become subdivided by the development of false septa stretching across, must be regarded as typical of the Order—as in Bentham and Hooker's group Pedalicae. Others with ovaries unilocular and plurilocular to be regarded respectively as distinct forms with different origin, and as forms derived from such as have the typical bilocular arrangement, as will appear in the sequel.

In *Pedalium* and *Pterodiscus* the ovary is bilocular, with two pendulous ovules in each loculus attached to the septum right and left of the median line as in Trapella. In Harpagophytum, which is placed in the same group, we find the same characters, combined with numerous ovules. Our plant I believe comes nearest to Pedalium, differing in its aquatic habit and semi-inferior ovary. If this surmise be correct, Trapella must have diverged early—whilst yet its ovary was superior and both loculi were fully developed. This state of things has persisted in *Pedalium*, but in *Trapella*, for reasons to be considered hereafter, the ovary has become adherent and the anterior loculus rudimentary.

The tribe Pretreeae have also probably diverged from the same centre, and Pretrea shows a strong resemblance to

under Gesneraceae) a tribe of Scrophulariaceae—Sesameae, under which the genera are given without any further subdivision of the tribe. The only reference to Trapella is in a foot-note, where it is spoken of as a genus of doubtful affinity. In this place, with the results of an investigation of complete material before me, I try to show its close relationship to Pedalium. Baillon had only the incomplete account (Hook. Ic. Pl. 1595), made from the first specimens which arrived, to go by.

¹ For convenience, the arrangement of the genera adopted by Bentham and Hooker in the Genera Plantarum is given here.

TRIBE I .- Martynieae.

- I. Martynia.
- 2. Craniolaria.

TRIBE III.—Sesameae.

- 6. Rogeria.
- 7. Sesamothamnus.
- 8. Sesamum.
- Ceratotheca.

TRIBE IV .- Pretreeae.

- 10. Pretrea.
 - 11. Linariopsis.
- 12. Josephinia.

TRIBE II .- Pedalieae.

- 3. Pedalium.
- 4. Pterodiscus.
- 5. Harpagophytum.

Pedalium on the one side, and Trapella on the other; this is seen especially in the form of the leaves and in the general habit; it must however be remembered that Pretrea is adapted to an arid climate. The greatest difference is shown by the fruit, which is primarily bilocular with erect basal ovules; partitions are developed as outgrowths from the median wall, which, becoming forked before meeting the dorsal and ventral walls of the fruit, divide each loculus into three compartments. The compartments lying right and left respectively are fertile, but the median compartment of each loculus is empty.

The genera included in the tribe of the Sesameae are to be derived from the Pedalieae through the genus Harpagophytum. Baillon has pointed out that in H. Grandidieri dorsal and ventral ingrowths arise, which do not reach the placenta at any stage. This I can confirm for the species in question, and find that Decaisne 2 figured it for H. Zeyheri. In the recently created genus, Holubia, Oliv.3, which is placed in the tribe Pedalieae, it seems that there is also a tendency to dorsal and ventral ingrowths of the ovary wall; these, however, do not reach the placenta. Doubtless Holubia is nearly allied to Harpagophytum, though its fruit is as yet unknown. It may be a link between Pedalium and Harpagophytum. In this way the completely divided loculi of Sesamum and Rogeria are foreshadowed, as indicated by Baillon (loc. cit.). It is only necessary to conceive the false septa of Harpagophytum fusing completely with the axile placenta to give us the four locelli, each bearing numerous ovules along its inner angle, of Sesamum and its allies. In Rogeria, it should be mentioned, the two anterior compartments are much larger than the posterior, the latter containing only a few, sometimes no seeds.

¹ H. Baillon, Notes sur les Pédalinées in Bulletin mensuel de la Soc. Linn. de Paris, No. 84 (1887), p. 665.

² Decaisne, Revue du groupe des Pédalinées, pl. ii. fig. 6, in Annales d. Sc. Nat. Bot. 5 sér. T. iii.

³ D. Oliver, in Hook. Ic. Pl. tab. 1475.

The genera *Martynia* and *Craniolaria* deviate entirely from the type of Pedalineae, from which all the others can be derived. In them placentation is parietal; and, as Baillon has pointed out, they may reasonably be removed from Pedalineae to be placed perhaps with Gesneraceae. Such a severance from Pedalineae is strengthened when we consider that these two genera alone are American—all other Pedalineae being Old-World. As above stated, Gesneraceae are, with the exception of the Cyrtandreae, which belong to both, also New-World.

Passing on to *Trapella* itself. In it we find a genuinely axile placenta, and no trace of any tendency to develop false partitions. As in *Rogeria*, one loculus has become much reduced; in *Rogeria* it is the posterior, in *Trapella* the anterior. This is to be regarded only as an instance of abortion of one ovary-cell arising independently in the same Natural Family, not as indicating a very close affinity between *Trapella* and *Rogeria*. *Trapella*, in its pendulous ovules and primarily bilocular ovary, approaches *Pedalium*. Even in its rudimentary loculus we find in *Trapella* what may very well be regarded as a rudimentary ovule (p. 82). The essential points of distinction depend perhaps upon its ovary being semi-inferior, for correlated with this, it may be, are all the peculiarities at issue.

It is an important thing to notice that *Pedalium* is not limited to S. Africa, as are so many of the other genera. It is a native also of Eastern India, and this brings it into relation with *Trapella*, a native of Central China (Ichang) and Japan. *Trapella*, I believe, has originated from the *Pedalium* stock, and adapting itself to an aquatic mode of life, has become profoundly modified. The tendency of the ripening seed (only one of the two ovules ever develops into a seed) to elongate downwards may perhaps have been an important factor in the initiation of great floral changes. The ancestral superior ovary, it may be supposed, has become invaginated into the receptacle, and its extension, in a downward direction, very greatly increased to accommodate the enlarging seed.

Comparing the ovary in the young bud (Fig. 17) and in the mature flower (Fig. 15), it is unquestionable that that part which is inferior (i.e. below the insertion of the calyx) constitutes a much larger proportion of the whole ovary in the flower than in the bud; and this difference is more marked in the fruit. The elongation of the fertilized ovule would appear to be extremely rapid (see p. 89), and due, to a great extent, to the active growth of the lower apical tissue of the ovule.

It being, for some reason, advantageous for this stage (i. e. the elongation of the ovule and development of the endosperm) to be rapidly passed through, it is not surprising to find developed a special organ, by means of which ultimately the embryo is enabled to make use of the food contained in the lower ovular tissue. Hence we find (1) the absorptive organ, in this case formed from the modified apical cap-cell, at an early period filled with transitory starch-grains; (2) the endosperm growing at the expense of the surrounding tissue, from which nourishment is absorbed, partly direct and partly by the special absorptive organ in question; (3) the embryo growing at the expense of the endosperm.

Finally, the fact of the prominent spines being in *Trapella* borne by the invaginated part of the fruit, whilst in *Pedalium* they arise from a superior fruit, is obviously correlated with the grand modifications undergone in the floral relations.

The possession still in the ripe seed of a thin layer of endosperm points towards, rather than away from, the Pedalinaceous affinity. The Order is usually given as 'exalbuminous,' and *Trapella* itself even was at first described as such; for, from the reduction of the integument to a single layer of flattened cells, it was impossible then without embryological evidence to say that the described testa was not such in reality. But not only is the seed of *Trapella* provided with several layers of endosperm, but in *Pedalium* ¹ also a like state of things exists. Indeed were investigation pushed further in the same direction,

¹ Baillon in the new part of his Histoire des Plantes (vol. ix. p. 444) describes the endosperm in this genus—'albumine membraniformi.'

other genera would probably be found not really entirely 'exalbuminous'.

Hence, then, although at first sight the gap between *Trapella* and *Pedalium* appears a wide one, still when we consider that *Trapella* has entirely changed its habit of life and lived under fresh conditions, it is not difficult to understand that the relationship may be a close one, though the differences be considerable.

The alternatives to placing *Trapella* in Pedalineae would be to place it in Myoporineae, or to make it the type of a new Natural Order. Such a course as that of founding a new Natural Order would be, in the present state of bilabiate Monopetalae, ill-advised ².

Trapella must thus rest in Pedalineae, forming the only genus in a new tribe, Trapelleae. Following the 'Genera Plantarum' classification, this will make five tribes in all. (See footnote, supra, p. 106.)

Though coming in touch with Myoporineae in the form and arrangement of the seeds, it is separated therefrom by its eminently Pedalinaceous fruit and opposite leaves. None the less *Trapella* forms a connecting link between the two, somewhat artificially separated, cohorts of the Genera Plantarum, namely the Personales and the Lamiales; Pedalineae being placed with the former, Myoporineae with the latter.

In conclusion, I wish to express my indebtedness to my father, at whose suggestion this work was undertaken, and to Mr. Thiselton Dyer, for his warm interest, and for the many facilities which he has afforded me.

Miss Matilda Smith has kindly drawn for me figures 1-7 on Plate V.

¹ This I find to be the case in *Pterodiscus*, *Rogeria* and *Linariopsis*, in addition to *Pedalium*.

² The arguments against investing an aberrant monotypic genus with the dignity of a separate Natural Order have been very succinctly stated by Sir Joseph Hooker, in his paper on *Hydrothrix*, a new genus of Pontederiaceae, in this Journal, vol. i. pp. 91-2.

EXPLANATION OF FIGURES IN PLATES V, VI, VII, VIII, AND IX

Illustrating Mr. F. W. Oliver's Paper on the Structure, Development, and Affinities of *Trapella*, *Oliv.*, a new Genus of Pedalineae.

Fig. 1. General view of the plant, showing both floating and submerged parts. In several of the leaf-axils are fully developed fruits, and one flower (to the right) from which the corolla has fallen away. To the left is a submerged axillary shoot, bearing a young cleistogamic fruit. Nat. size.

Fig. 2. Shows two nodes of a submerged stem, with adventitious roots arising from them. To the right are two roots arising from the internode. Nat. size.

Figs. 3 and 4. Side and front views of a flower. α . β ., anterior petal; l. β ., lateral petals; β . β ., posterior petals. 2/1.

Fig. 5. The corolla laid open. α . p., etc., as in Figs. 3 and 4; sd., staminodes; sm., stamens. 2/1.

Fig. 6 a and b. Front and back views of a stamen. A-B, plane of section given in Fig. 23. 5/1.

Fig. 7 α and b. Front and back views of a staminode. 5/1.

Fig. 8. Front view of calyx, style and young spines after falling away of corolla. 2/1.

Fig. 9. The stigma from posterior face. 5/1.

Figs. 10 and 11. Front and back views, respectively, of ovary, whilst corolla is still in situ, showing relations of calyx-lobes to the young ovarian spines. a.s., anterior spine; l.s., lateral spines; p.s., posterior spines. 3/1.

Figs. 12, 13, and 14. Young, medium, and adult fruits respectively. The calyx-lobes have closed over the ovary. $\alpha.s.$, anterior spine; $\ell.s.$, lateral spines; $\rho.ss.$, posterior spines. Slightly enlarged.

Fig. 15. Section of a flower, showing insertion of calyx-lobes, corolla, ovules, etc. a.s., rudiment of anterior spine; cal., calyx-limb; cor., corolla; loc., functional loculus of ovary; ov. 1, upper sessile ovule; ov. 2, lower stalked ovule; red. l., rudimentary loculus; sl., style. 2/1.

Fig. 16. Longitudinal section of a young bud, made in the antero-posterior plane. The insertion of the upper ovule only is given, that of the lower not being in the plane of section. The calyx is invested outside with a dense covering of quadrifid glands. The vascular bundles are shaded. cal., calyx; cor., corolla; loc., the fully-developed loculus; ov. 1, the upper ovule: red. l., the rudimentary loculus. 25/1.

Fig. 17. Longitudinal section of a bud of same age as Fig. 16, but made at right angles to the antero-posterior plane, so as to show the insertion of the stamens. The section passes through the fully-developed loculus only. p. m. c., pollen mother-cells; tap., tapetal layer: other references as in Fig. 16. 25/1.

Fig. 18. Upper part of ovary, with right side removed, to show the insertion of the two ovules. fun., funicle of lower ovule; ov.¹, upper sessile ovule; ov.², lower stalked ovule; r., cellular emergence, possibly representing a rudimentary ovule; red. l. reduced loculus. 45/1.

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Fig. 19. Longitudinal section, slightly to right of antero-posterior median plane, showing insertion of upper ovule, ov. 1 e. s., embryo-sac, with two cap-cells below it; m., mycropyle. 45/1.

Fig. 20. Similar section, slightly to left of median plane, showing insertion of lower stalked ovule, ov. 2 45/1.

Fig. 21. Longitudinal section of a cleistogamic flower, with stigma sessile on the ovary. a.l., anterior lobe of stigma; p.l., posterior lobe, which is reduced. Note that the reduced stigmatic lobe corresponds to fully-developed loculus of ovary and conversely. 45/1.

Fig. 22. Antero-posterior section of stigma, and upper part of style. a.l., anterior lobe; p.l., posterior lobe; v.h., vascular bundles.

Fig. 23. Transverse section (A-B of 6b) of anther after dehiscence. con., connective; f. L, fibrous layer. 70/1.

Fig. 24. Very young upper ovule, ev.1, showing the nucellus and origin of thick integument. In the nucellus is the embryo-sac mother-cell, and one cell (c) lying below it, which has just been cut off from its lower end. ct., integument; e.s.m.c., embryo-sac mother-cell. 480/I.

Fig. 25. Embryo-sac, with three equal cap-cells (c^1, c^2, c^2) , lying below it. Section taken from a flower not yet opened. 400/1.

Figs. 26 and 27. Two sections of upper ovule, showing the embryo-sac, e. s., and three cap-cells (c^1, c^2, c^3) , below it, together with the surrounding tissue of the ovule. In 26 the uppermost cap-cell, c^1 , is becoming obliterated; in 27 the lowermost, c^3 , is much larger than either c^1 or c^2 . In 27 notice also the pointed summit of the embryo-sac, where it abuts upon the micropyle, m. 450/1.

Fig. 28. Embryo-sac at time of fertilization. The lowermost cap-cell is now much larger than c^1 or c^2 . In the micropyle is seen a pollen-tube, p.t. anti, antipodals; c^1 , c^2 , c^3 , cap-cells; e., egg-cell; e.s., embryo-sac; n.e.s., definitive nucleus of embryo-sac; p.t., pollen-tube; syn., synergidae. 450/1.

Fig. 29. Embryo-sac, e. s., and cap-cells, c^1 , c^2 , c^3 , from the lower ovule at a slightly later period than that in 28. Notice especially that the lowermost cap-cell, c^3 , has elongated considerably, c^1 and c^2 remaining quite small. Only one nucleus was observed in the embryo-sac in this preparation, the others very probably being in another section, or fallen away. The figure is given, however, to show the elongated cap-cell, c^3 . 400/1.

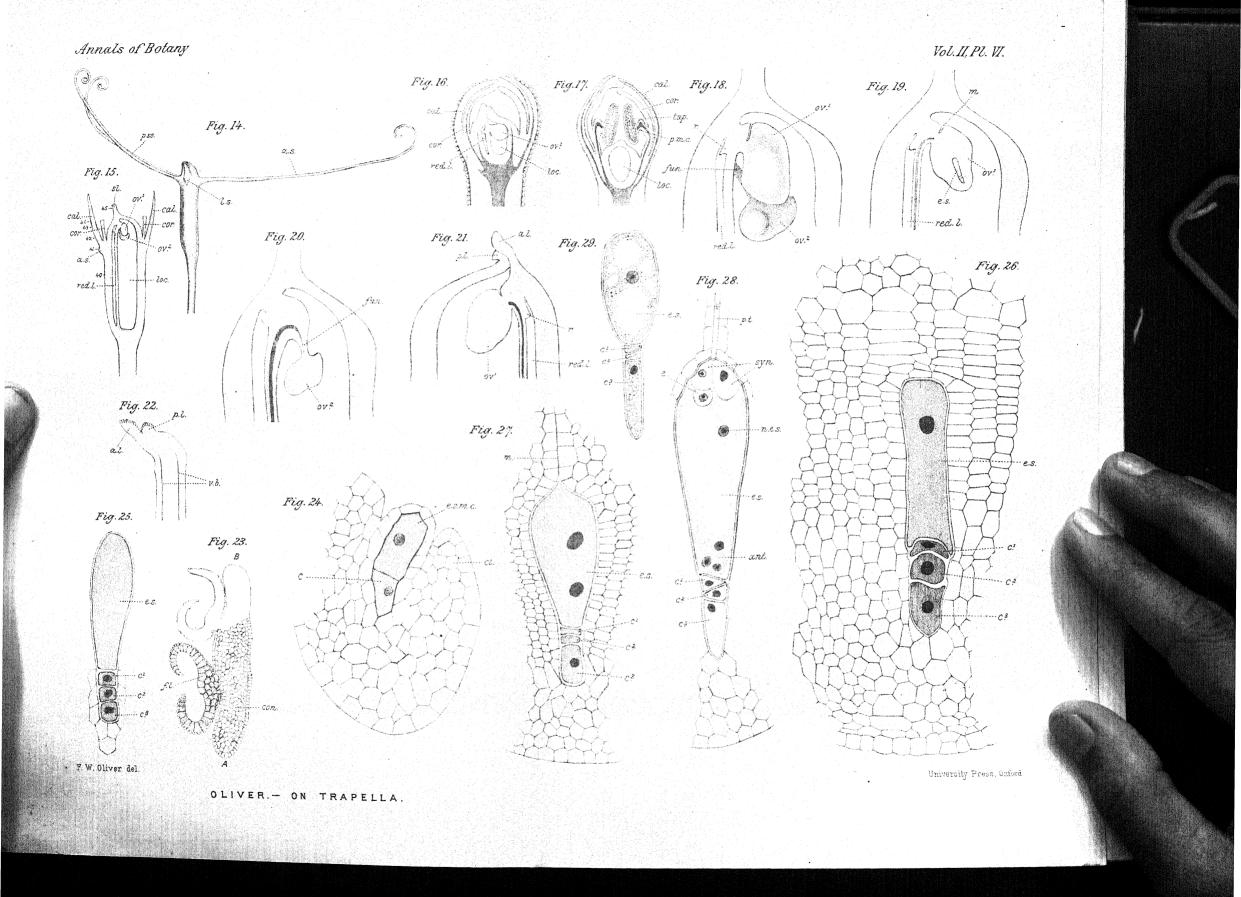
Fig. 30. Shows the ovule and embryo-sac soon after fertilization, The terminal cap-cell, c^2 , has become divided longitudinally, and now forms a large appendage to the embryo-sac. The egg-cell has developed into a suspensor terminated by an undivided embryo-cell. Large endosperm cells have already arisen within the embryo-sac. The ovule has elongated downwards considerably. c^2 , the divided and much enlarged terminal cap-cell; *emb.*, embryo; *end.*, endosperm; m., micropyle; sp., suspensor; syn., synergidae; a.s., ant. spine. 150/1.

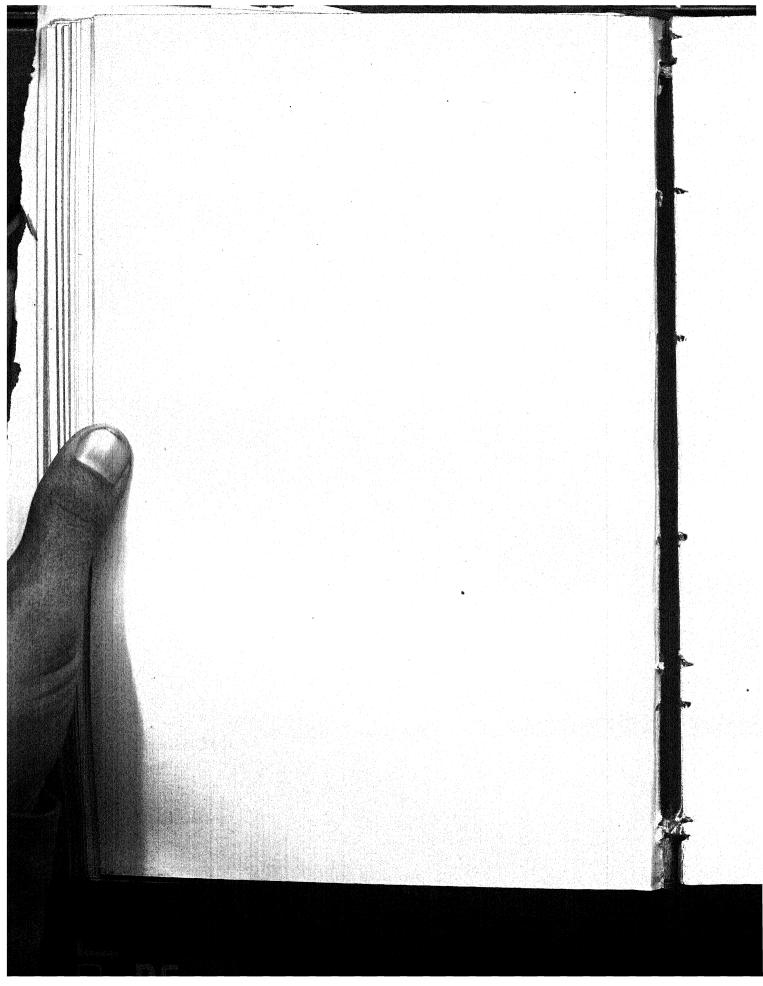
Figs. 31 and 32. Somewhat later stages than that given in 30; references as before. Fig. 31, 30/1; Fig. 32, 22/1.

Fig. 33. Enlarged view of section of appendage, c^3 , in Fig. 32. The base of the embryo-sac with endosperm, *end.*, is seen, with the probable remains of the intermediate cap-cells, c^1 and c^2 , between it and c^3 . The nuclei are large and



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granular. In the figure the upper part of the appendage only is given; its pointed end is continued some distance down. 255/1.

Fig. 34. A somewhat shorter appendage than that in Fig. 33. The section is perpendicular to that in Fig. 33, and a proliferation of endosperm cells has grown over its proximal part.

Fig. 34 α . Shows the nucleus of one of these cells beginning to fragment. 250/1.

Fig. 35. Longitudinal section of mature seed in situ. Section passes through antero-posterior plane. The embryo now occupies the greater part of the embryosac. It is surrounded by a thin layer of endosperm, end. Only one cotyledon, cot., is seen, since the cotyledons lie right and left of the antero-posterior plane. The appendage, c^3 , is seen at the base of the seed, attached to the embryo-sac; rad., radicle; cal., calyx; a. s., anterior spine; sl., style. 10/1.

Fig. 35 α . Shows the embryo seen in section, at right angles to that in Fig. 35. The extent of the cotyledons is seen. 10/1.

Fig. 36. Longitudinal section of the upper part of a ripening seed, passing through the antero-posterior plane. The embryo, emb., and suspensor, sp., are seen in situ, surrounded by endosperm, emd. The upper part of the embryo-sac is dilated, and contains a vacuolated protoplasm with conspicuous nuclei. This vacuolated mass, syn., represents the altered synergidae. The upper endosperm cells, L.d., are arranged in more or less horizontal strata; these becoming lignified later form the lignified diaphragm referred to on p. 93. a. sp., point of attachment of suspensor to embryo-sac wall; emb., embryo; end., endosperm; int., integument (and nucellar tissue) of ovule; L.d., lignified diaphragm; m., micropyle; pc., pericarp; sp., suspensor; v. b., vascular bundle. 110/1.

Fig. 37. Longitudinal section of top of adult seed, similar to Fig. 36. The endosperm and enlarged synergidae have encroached still more upon the integument, which is reduced to a single layer of cells throughout the greater part of the seed. The synergidal region has a curious mottled effect; the upper part of the suspensor is seen running obliquely downwards across it. The embryonic root is seen just below the lignified diaphragm, l. d. e., epidermis of root; d. c., dermato-calyptrogenic layer; pb., periblem; pl., plerome; other references as in Fig. 36. 100/1.

Fig. 38. Enlarged view of the region in the neighbourhood of A in Fig. 37. The curious mottling of the synergidal region is shown, and the disintegrated looking and granular nucleus (n.), in a special area of its own, n. a. The lignified diaphragm is drawn in dark, l. d. 300/1.

Fig. 39. Longitudinal section of the supposed rudimentary ovule, r., which projects into the reduced loculus, red. l. 135/1.

Figs. 40, 41, 42, 43, 44, and 45 are transverse sections of a flower at different heights indicated by the numbers 40-45 in Fig. 15. Fig. 40 is taken half-way down the ovary; Fig. 41, at the insertion of the emergences; Fig. 42, just above the insertion of the calyx (the corolla has fallen away, and is not represented); Fig. 43, at the insertion of the lower ovule, ov.²; Fig. 44, at the insertion of the upper ovule, ov.¹; Fig. 45 is a transverse section of the style. The vascular bundles are coloured:—green to the calyx-lobes; red to the corolline-lobes; brown to the emergences (these originate from the corolline bundles, red just below the insertion of the emergences); yellow to the stamens and staminodes (the position marked x in Figs. 40 and 41 is that which would be occupied by a bundle to

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aborted posterior stamen if it were present); blue to the carpels. loc., fully-developed posterior loculus; red. l., reduced anterior loculus; r., rudimentary ovule in the reduced loculus (cf. Fig. 43).

Fig. 46. Outline of embryo and suspensor from a young seed, slightly older than that given in Fig. 36. cot., cotyledons; sp., suspensor.

Fig. 47. Median longitudinal section through the apex of radicle, of about same age as that in Fig. 46. e., epidermis; d. c., dermato-calyptrogenic layer; pb., periblem; pl., plerome; sp., suspensor.

Fig. 48. The ripe seed in situ. ap., pocket-like outgrowth of testa, in which is inserted the appendage, c³; syn. tub., synergidal tubercle. The reduced loculus is represented by a dotted line. Nat. size.

Fig. 49. Transverse section of a floating stem. cor., cortex; ens., endodermis; ep., epidermis; i., intercellular spaces; ph., phloem; v., vessels. 70/1.

Fig. 50. Transverse section of submerged part of stem, showing larger intercellular spaces. References as in Fig. 49. 70/1.

Fig. 51. Transverse section of the axial-cylinder of the stem. *ens.*, endodermis; \hat{z} , s., intercellular spaces in the 'pith,' due to breaking down of vessels; ph., phloem; s, t, sieve-tubes; v., vessels of xylem. 120/1.

Fig. 52. Transverse section of peripheral part of cortex from a node, showing the thick-walled cortical-cells, with intercellular spaces (i.s.) between. c.b., meristem formed from sub-epidermal layer; ep., epidermis; gl., quadrifid gland. 240/1.

Fig. 53. Transverse section of an adventitious root, showing the large radially-arranged intercellular spaces. Several of the radial rows of cortical cells have collapsed, and are represented merely as lines. References as in Fig. 49. 70/1.

Fig. 54. Transverse section of the axial cylinder of an adventitious root; it is essentially tetrarch. ens., endodermis; ph., phloem; vv., vessels of xylem. 240/1.

Fig. 55. Longitudinal section of a sieve-tube from the stem. cc., companion cell; s. k, schlauch-kopf; s. p., sieve-plate. Much enlarged.

Fig. 56. Similar section of one of the outer obliterated sieve-tubes. c. p., callusplate.

Fig. 57. Diagrammatic transverse section at a node, showing the entrance of leaf-bundles. A and B, groups of anastomosing vessels; adv. rt., adventitious roots; l. tr., united bundle of leaf traversing the cortex; pet., petiole.

Fig. 58. Vertical section through the edge of a floating leaf to show a water-gland. e., epithem; v. b. e., ending of vascular-bundle in the gland; w. p., water-pore.

Fig. 59. The water-pore, w. p., seen from above.

Fig. 6o. Epidermis of upper side of floating leaf, showing stomata, st., and one eight-celled gland, st. The dotted lines below st. indicate the walls of the epidermal cells seen through.

Fig. 60 α . Epidermis of lower side, with four-celled glands, gl., and the pedicels of glands which have fallen away, gl^{1} .

Fig. 61. Eight-celled gland from floating leaf, drawn to larger scale.

Fig. 62. A form of stomate occasionally met with at the edge of the leaf, in the immediate neighbourhood of a water-gland.

Fig. 63 a. Outline of submerged leaf. Nat. size.

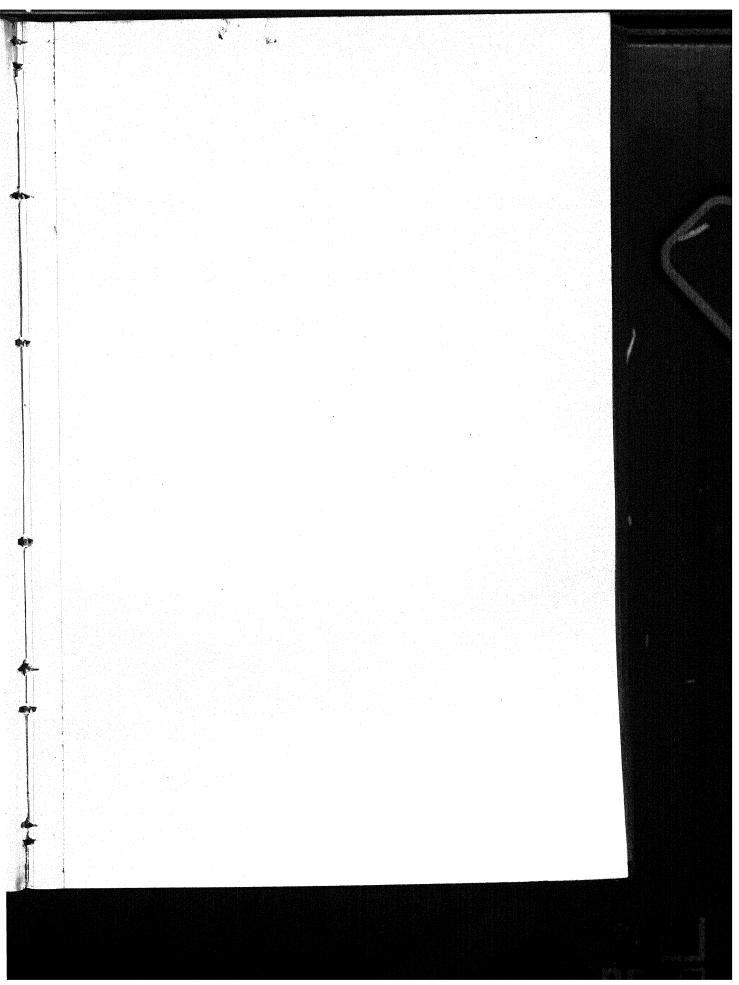


Fig. 51.

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Fig. 52.

Fig. 63 b. Similar outline of leaf, intermediate in form between a submerged and floating leaf. Nat. size.

Fig. 63 c. Two teeth from a submerged leaf seen under a low magnifying power, so as to show the course of the vascular bundles as they run to the waterglands, zv. g.

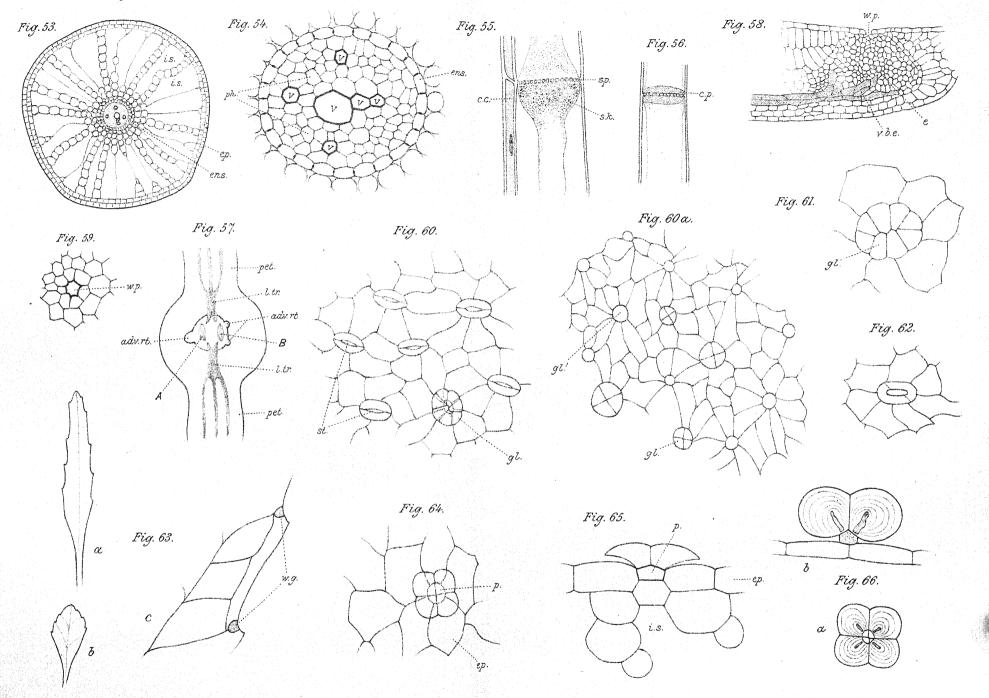
Fig. 64. Epidermis of submerged leaf, showing four-celled glands. ep, epidermal cells; p, pedicel of gland (dotted outline).

Fig. 65. Vertical section of same gland. i.s., intercellular-space; p., pedicel of gland.

Fig. 66 α and b. Pretrea; four-celled gland from leaf, seen from above, and in section, for comparison with Figs. 64 and 65.

APPENDIX.

- (1) Since this paper has been in proof, Dr. Vines has kindly called my attention to the similarity presented by the sucker or appendage described above and the cotyloid cell of Avicennia (vide M. Treub, in Annales du Jardin Botanique de Buitenzorg, vol. iii, 1883, p. 79). The cotyloid cell resembles the 'appendage' of Trapella in being a 'feeder,' and also in its origin—in that it originates outside the embryo-sac. Whether the cotyloid cell be a cap-cell or not remains to be shown. The cotyloid cell is seen, after the commencement of the development of endosperm, lying beside the embryo-sac (loc. cit. Pl. XIV, Fig. 18), to which it may be a sister cell. This remains to be shown.
- (2) In one of his letters, Dr. Henry mentions that in the Chinese illustrated Botany 'Chi Wu Ming,' vol. xvii, folio 43, an aquatic plant somewhat resembling *Trapella* is figured. This plant is known as 'Chi-Mi' in the province of Chi-li, and 'Ch'a ling' (i.e. Tea Trapa) in the province of Honan. The description is too incomplete for any decision as to its affinity to be made, and the figure (of which Dr. Henry encloses a tracing) shows a plant with habit somewhat recalling *Trapella*, but with leaves alternate, and pseudopodial branching.





NOTES.

ON THE SYSTEMATIC POSITION OF ISOËTES, L.-

The systematic position of this genus has been the subject of much speculation on the part of botanists. By some it has been placed among the Phanerogams¹, by others among the Mosses², and by the majority among the Vascular Cryptogams, the last being undoubtedly its true position. There has also been considerable difference of opinion as to its place among the Vascular Cryptogams. The earlier botanists all associate Isoètes with Pilularia and Marsilea. Thus Linnaeus³ associates these genera as a group of the Filices having 'fructificationes radicales,' and Gleditsch⁴ assigns to Isoëtes a similar position. The affinity of Isoëtes with Pilularia, Marsilea, Salvinia, and Azolla, is affirmed more definitely by Willdenow⁵, who associates them in the group Hydropterides; and by Batsch⁶, who unites these genera in the group Rhizocarpae, as does also Bischoff⁷. Bartling⁸ takes the same view, classifying the Rhizocarpae into the three orders, Salviniaceae, Marsiliaceae, and Isoëteae.

On the other hand, De Candolle⁹ removes *Isoëtes* from the Rhizocarpeae, the group being now termed Rhizospermae, and incorporates it with the Lycopodiaceae, on the following grounds: 'Ce genre semble se rapprocher, par son port, des rhizospermes, mais il touche réellement aux lycopodes; 1º par ses fructifications axillaires, et non

¹ Reichenbach (Conspectus, 1828) places *Isoëtes* together with Potamogetoneae and Aroideae in a group', which he terms Limnobiae. Adanson (Fam. des Plantes, 1763) makes it a genus of Aroideae.

² Dillenius (Hist. Musc. 1741) places *Isoètes*, together with *Pilularia* and *Subularia* in the Musci, under the name *Calamaria*. B. Jussieu (Ht. Trian. 1759) also places it among the Mosses.

3 Linnaeus, Systema Vegetabilium, 1751.

* Gleditsch, Syst. Plant. 1764.

⁵ Willdenow, Bem. Farrenkräuter, 1802; Species Plantarum, t. v, 1810.

Batsch, Tab. affinitatum Regni Vegetabilis, 1802.
 Bischoff, Die Kryptogamischen Gewaechse, 1828.

⁸ Bartling, Ordines Naturales Plantarum, 1830.

⁹ Lamarck et A. P. de Candolle, Flore Française, t. ii, 1815 (Lycopodiaceae, fam. Monocotyledonum cryptogamarum).

pas proprement radicales; 2º par l'existence des deux genres de coques qu'on trouve dans plusieurs lycopodes, savoir, les coques à poussière et les coques qui portent des globules chagrinés et munis de trois côtes rayonnantes à leur base.' In this he is followed by Brongniart¹. Endlicher², recognising the affinity between Isoëtes and the Lycopodiaceae, does not, however, unite them, but founds the class Selagines which includes the two orders Lycopodiaceae and Isoëteae. The attitude of Lindley on this point is curious. In his Natural System of Botany (Ed. 2, 1836) he follows De Candolle in including Isoëtes in the Lycopodiaceae, founding at the same time the cohort Lycopodales, consisting of the orders Lycopodiaceae, Marsiliaceae, and Salviniaceae; whereas in his later works (Vegetable Kingdom, Ed. 2, 1846, Ed. 3, 1853), he removes Isoëtes from the Lycopodiaceae and places it, with Marsilia, Pilularia, Salvinia, and Azolla, in an order Marsiliaceae. Payer3 retains Isoëtes in the Lycopodiaceae, uniting it with Psilotum and Tmesipteris in the group Psiloteae. Berkeley4 says with regard to it, 'on the whole, therefore, notwithstanding the difference in tissue, it should seem that it is a true Lycopod.'

The next important step in the classification of the Vascular Cryptogams was made by Sachs. Recognising the importance of distinguishing the homosporous (or isosporous) from the heterosporous forms, and at the same time overestimating it, in the three earlier editions of his Lehrbuch, he divides the Vascular Cryptogams into two groups, the isosporous, containing Filices, Equisetaceae, Ophioglosseae, and the heterosporous, containing the Rhizocarpae and the Lycopodiaceae, pointing out at the same time that, among the Lycopodiaceae, heterospory only occurs in the Selaginelleae and Isoëteae. The fourth edition of the Lehrbuch⁵ (1874) shows a marked advance. The classification here adopted brings to light the appreciation of the fact that heterospory has arisen within the limits of the several groups, each group (ex. Equisetaceae) therefore including both heterosporous and homosporous forms; the Rhizocarpae are recognised as the heterosporous forms of the Fern-alliance,

⁵ English edition, Oxford, 1882.

¹ Ad. Brongniart, in Dict. Classique d'Hist. Nat. t. ix, 1826.

Endlicher, Genera Plantarum, 1836-40.
 Payer, Botanique Cryptogamique, 1850.

⁴ Berkeley, Introduction to Cryptogamic Botany, 1857.

and the Selaginelleae and Isoëteae, united into the group Ligulatae, as the heterosporous forms of the Lycopodium-alliance. It is as follows:—

Class I, Equisetaceae.

" II, Filicinae.

Order 1. Stipulatae (incl. Ophioglosseae, Marattiaceae, Osmundaceae?, Schizaeaceae?).

" 2. Filices.

" 3. Rhizocarpae.

" III, Dichotomae.

Order 1. Lycopodiaceae (Lycopodieae, Psiloteae, Phylloglosseae).

" 2. Ligulatae (Selaginelleae, Isoë-

In the edition of the systematic portion of the Lehrbuch by Goebel¹, the classification is in the main adhered to, though with some Thus, the class Equisetaceae is reconstituted as Equisetinae, certain heterosporous fossil forms probably belonging The orders of the Filicinae are to this group being included. arranged in two groups in accordance with the results of Goebel's researches on the development of the sporangia: the majority of the Ferns being grouped with the Rhizocarpae (now termed Hydropterideae) as Leptosporangiate Filicinae, the remainder (Ophioglosseae, Marattiaceae) constituting the Eusporangiate Filicinae. Sachs' class Dichotomae is re-named Lycopodinae2, as Sachs' name is misleading. There are three orders of Lycopodinae: Lycopodiaceae (Lycopodium, Phylloglossum), Psilotaceae (Psilotum, Tmesipteris), Ligulatae (Selaginelleae, Isoëteae). The proposal is made to distinguish homosporous and heterosporous forms in the order Lycopodiaceae, the heterosporous forms being represented by the fossil genus Lepidodendron, but the value of this is questionable. Selaginella

¹ Goebel, Grundzüge der Systematik, 1882; Outlines of Classification and Special Morphology, Oxford, 1887.

² It should be borne in mind that the term Lycopodinae had been previously used in a different sense by Link (Enumeratio, 1822) as the equivalent of Lycopodiaceae of De Candolle. The order Lycopodineae was founded by Swartz (Syn. Fil. 1806) to include the genera *Lycopodium*, *Tmesipteris*, and *Psilotum*, and this term has since been used in many different senses by various writers.

appears to be the real heterosporous form corresponding to Lycopodium, and probably the fossil heterosporous Lycopodinous forms belong really to the Selaginelleae.

Although this position of *Isoètes* has met with general acceptance, yet it is a question whether it really corresponds to its true affinities. Goebel himself says¹, 'The groups which have been brought together under the name of Ligulatae have scarcely anything in common but the presence of a ligule, and it would be better perhaps to make separate divisions of them.' But if there is little in common between the Isoèteae and the Selaginelleae, there must be still less in common between *Isoètes* and the Lycopodiaceae. The question at issue is, therefore, not merely whether the Selaginelleae and the Isoèteae should be separated, but whether *Isoètes* really belongs to the Lycopodinae at all. This raises the further question; if *Isoètes* be removed from the Lycopodinae, with what group of Vascular Cryptogams shall it be associated? It is the object of the present note to endeavour to answer these questions.

Taking first the question of the affinity of Isoëtes with the Lycopodinae, it becomes at once apparent that there are many important differences between them. The general characteristic of the sporophyte of the Lycopodinae is that the stem is slender and much branched, the leaves being small and numerous: in Isoètes, on the contrary, the stem is short, thick, and unbranched, and the leaves are relatively large. It is true that in habit Phylloglossum more nearly resembles Isoètes than it does the other Lycopodinae; but even here² there is a branching of the stem, at least in the sporangiferous forms, in connexion with the formation of the tubers. Again, the sporangia of the typical Lycopodinae are borne on sporophylls which are confined to special branches; and in the majority the sporophylls differ from the foliage-leaves and are aggregated together into cones on special shoots: in *Isoètes* all the foliage-leaves are sporangiferous. Further, so far as the embryogeny of the sporophyte is known in the Lycopodinae, that is, in the case of Lycopodium and Selaginella. there is a suspensor but no primary root; whereas in Isoëtes there is a primary root but no suspensor. As regards the gametophyte, the mode of germination of the microspores is much the same in Isoëtes

1 Outlines, p. 196.

² Bower, On the development and morphology of *Phylloglossum Drummondii*, Phil. Trans. II, 1885.

and in Selaginella, but there is the well-known difference in the germination of the macrospores.

These differences between *Isoèles* and the recognised members of the Lycopodinae are surely sufficiently striking to raise a doubt as to the propriety of continuing to include them all in one group, and thus the question is raised as to what other position can, with any probability, be assigned to *Isoèles*.

In its general habit, and in the absence of sporangiferous cones and specially differentiated sporophylls, *Isoètes* resembles the Filices, as also in the more general features of its embryogeny. This relationship is emphasised in a remarkable manner if, as Sadebeck suggests¹, the velum of *Isoètes* be truly homologous with the indusium present in many Filices and in the Salviniaceae. It must be admitted, however, that both the male and female gametophytes of *Isoètes* resemble rather those of *Selaginella* than those of the Hydropterideae.

The general tendency of these remarks would seem to be towards a reunion of *Isoètes* with the Rhizocarpae; but in view of Goebel's researches on the development of its sporangium this cannot be done. Isoëtes is distinctly eusporangiate, whereas the Rhizocarpae are as distinctly leptosporangiate. If Isoëles is to be included in the Filicinae, it must be connected with the eusporangiate forms of that This is, in fact, the answer to the question as to the systematic position of Isoètes, if removed from the Lycopodinae: it is a heterosporous form, the only one hitherto recognised as such, of the Eusporangiate Filicinae. It certainly resembles the Ophioglosseae and the Marattiaceae in its general habit; in Isoëtes as also in these forms the stem is remarkable for its extremely small longitudinal growth, for the consequent absence of internodes and of branching, for the entire concealment of its surface by the insertions of the leaves, and for the formation of roots in acropetal succession close behind its apex. There is a more special point of resemblance, though it may amount to no more than an analogy, between the imperfectly multilocular sporangia of Isoëtes and the compound sporangium of most of the Marattiaceae.

Doubtless, many objections will be raised to this view of the

¹ Sadebeck, Die Gefässkryptogamen, in Schenk's Handbuch der Botanik, I, p. 326 k, 1879.

systematic position of *Isoètes*, some of which I will now endeavour to meet by anticipation.

In the first place, it may be objected that, in the growth in thickness of its stem, *Isoèles* differs from the Filicinae and indicates a relationship with the extinct Lycopodinae. In reply to this it may be pointed out that secondary growth in thickness of the stem is by no means a peculiarly Lycopodinous character; and further, that some indication of such secondary thickening is to be found in the rhizome of existing Ophioglosseae.

Secondly, the absence of a single apical cell in the growing-point of either stem or root may be urged as an objection to the incorporation of *Isoètes* with the Filicinae. This is not, however, an objection of any weight; for among the Lycopodinae, on the one hand, the presence of a single apical cell is common in *Selaginella*, and among the Filicinae, on the other, the presence of a single apical cell is not universal, there being in the roots of the Marattiaceae a group of apical cells.

It may be added here that Russow¹ has already drawn attention to certain histological resemblances between *Isoèles* and the Ophioglosseae.

Further, the resemblance between the male and female gametophytes of *Isoètes* and *Selaginella* may be urged as a ground for keeping these genera together, and therefore also for retaining *Isoètes* among the Lycopodinae. It has been already pointed out that the two genera do differ in this respect, and it may be further suggested that the reduction of the gametophytes of *Isoètes*, as compared with those of the Hydropterideae, is just what might be expected in higher and lower groups of the same series. In fact, the comparison of the gametophytes of *Isoètes* and *Selaginella* rather supports the view that they are forms, not belonging to one group, but occupying corresponding positions in two different series: that is to say, that *Isoètes* occupies in the Filicinae the same relative position as *Selaginella* in the Lycopodinae.

The presence of a ligule in both *Isoètes* and *Selaginella* might also be brought forward as a reason for classing them together; but, when contrasted with the wide difference in the class-characters, the importance of this common feature is but small. Moreover, it

¹ Russow, Vergleichende Untersuchungen, Mém. de PAcad. imp. de St. Pétersbourg, sér. 7, t. xix, 1872, p. 192.

is easy to imagine that a ligule may have been developed in the Filicinae as it has been in the Lycopodinae, to say nothing of other groups of plants.

On summing up the evidence, it appears to be proved that there is quite as much resemblance between *Isoètes* and the Eusporangiate Filices, as there is between *Selaginella* and the Lycopodiaceae; and further, that there is a closer resemblance between *Isoètes* and the Eusporangiate Filices than there is between *Isoètes* and the recognised Lycopodinae. At the same time, it must be admitted that there is some affinity between *Isoètes* and the Lycopodinae. But it has long been recognised that the Eusporangiate Filices are those Filices which have most affinity with the Lycopodinae; and, in uniting *Isoètes* with the former group, this affinity merely becomes more marked.

In conclusion, I would point out that the proposed change in the systematic position of *Isoètes* throws an altogether new light on the evolution of the Phanerogams from the Pteridophyta, but I reserve the discussion of this question for a future occasion.

S. H. VINES.

PRELIMINARY NOTE ON THE DEVELOPMENT OF THE ROOT OF EQUISETUM.—I undertook, as the result of some discussion with, and at the suggestion of, my friends Dr. Vines and Mr. Gardiner, to determine the somewhat doubtful point of the development of the double endodermis of the root of Equisetum. As I have not, at present, time to prepare a full account of my investigations I propose to give in this note the main results obtained.

The apical cell of the root gives rise to two kinds of tissue which can at once be distinguished from one another by the sequence of divisions. Of these, one forms an outer layer or cylinder constituting the *exomeristem* of Russow; the other is enclosed by it forming a central cord of tissue constituting the *endomeristem* of the same author.

The exomeristem is distinguished from first to last by its cells being arranged in radial rows, most distinctly so in the zone of cells immediately surrounding the endomeristem. The endomeristem may be said to be chiefly distinguishable by the fact that its cells are not arranged in radial rows, and are also smaller than the cells of the exomeristem. No one can possibly fail to see at the first glance where the line passes separating the two meristems. This is especially

the case at the later stages, for in the innermost layers of the exomeristem no more radial walls are formed, so that consequently the tangential diameter of these cells becomes very great. In the endomeristem, divisions having taken place freely towards the periphery, the junction of the tissues is made plain by the small-celled endomeristem abutting directly on the large-celled exomeristem. For some time the layer of exomeristem immediately surrounding the endomeristem remains unchanged, but eventually each cell of this layer divides radially by a tangential wall, thus making the layer double; it is these two layers which eventually form the double endodermis so well known in Equisetum. Roots of *E. hyemale*, L. were used. The material was hardened with picric acid and dehydrated with absolute alcohol; it was subsequently imbedded in hard parafin and sections cut with a microtome, the sections being carefully mounted in the order in which they were cut.

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PINUS MONOPHYLLA (Torrey and Fremont).—This is a species which differs from its congeners by its 'solitary glaucous terete leaves' (Sargent). Now, if the leaf were really solitary it would afford an illustration of a terminal leaf, the real existence of which has been denied. It must be remembered, however, that by some botanists the 'needles' of Pinus have been considered to be axial not foliar. Whether, however, there is any fundamental difference between axial and foliar structures is still to my mind a matter for doubt, but the point need not here be discussed, as for practical purposes, and especially for the purposes of this communication, I assume that the two are really different. As, moreover, the axial nature of the typical Pine needle is now pretty generally discredited it is not necessary here to allude to the matter further, but as Bertrand considers that the particular species now under discussion is exceptional, and that its 'needle' is really axial, it is advisable to cite what he says about it. 'C'est une sorte de rameau dont le cylindre ligneux s'est ouvert suivant une de ses génératrices, et s'est étalé sur un plan tangent diamétralement opposé à cette génératrice.' Engelmann² says 'it was

² Botany of California, II. (1880), p. 124.

¹ Annales des Sciences Naturelles, sér. 5, Tom. xx (1874), p. 102.

long considered probable that the terete leaf was in reality a connate pair, but the structure shows a single bundle, and therefore a single leaf.'

As it happens that the tree in question often does produce some of its leaves in pairs the probability mentioned by Engelmann did not seem remote, and Sir Joseph Hooker¹ adopted this view, saying that 'the anomaly in the foliage is due to the cohesion of the two semiterete leaves of each sheath by their adjacent faces, and is far from being a constant character. In the plants at Kew the two leaves are as often free as connate; and, on making a transverse section of any connate pair, it will be seen that the vascular bundle traversing the centre of the cylinder is, in fact, double, and that the two parts are sometimes separate.'

In the hope of reconciling the discrepancies between these statements, or of ascertaining which is the more correct, I have recently repeated some observations, which I made first in 1883, both as to the minute anatomy of these leaves and as to their mode of development. These observations are so readily checked, that it will be easy to confute or to confirm the conclusions at which I have arrived.

Alluding in the first place to the anatomy of the single cylindrical leaf, a transverse section through the middle shows that it is really, what it seems to be, a single leaf. The section is circular, the epiderm broken by stomata and consisting of more or less cubical cells, beneath which lies a double layer of thick-walled hypoderm. Close to the hypoderm and each surrounded by a girdle springing from it are the resin canals, two or three in number. Then comes the leaf-substance of several layers of polygonal cells filled with chlorophyll and with abundant starch grains. The outermost of these cells have sinuous walls, while the innermost are straight-walled and radiate in all directions from the bundle-sheath or endoderm. This latter sheath consists of a circle of ellipsoidal colourless cells filled with starch and surrounding the circular (in section) pericycle. The pericycle consists of ordinary colourless parenchymatous tissue, interspersed among which are some relatively very large libriform cells, while in the centre is the vascular bundle proper, in the form of a wide crescentic band, the convexity of which is directed towards the axis, the concavity in the opposite direction. The thick-walled xylem occupies the side nearest to the axis, the thin-walled, but relatively more abundant

¹ Gard. Chron. 1886, July 31, p. 136.

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phloëm being on the lower or outer side, a position indicative of the truly foliar nature of the body in question.

On the same shoot with these terete leaves are others arranged in pairs. The transverse section of either of these twin leaves, whether taken in the centre, at the base, or at the apex, shows a nearly semicircular outline, with the convexity beneath, the concavity above. The pericycle has the same general shape. In all other material points the structure is absolutely the same as in the terete leaves. Sir Joseph Hooker therefore examined a section of a 'connate pair,' and the vascular bundle he saw was really double—one portion belonging to one leaf, one to the other. My observations as to structure agree with those of Bertrand, as illustrated by him¹, and from them it will be seen that (form apart) the structure is in all essentials absolutely the same as in the leaves of other species of *Pinus*. The figure of the leaf-structure of *Pinus Strobus*, given on the same plate by Bertrand (fig. 10), shows how closely similar is the leaf-structure in the two species.

Anatomy then shows that the leaf-like body is a true leaf, which occurs singly, but occasionally in pairs. There is of course no difficulty in understanding the latter condition, the anomaly consists in the single cylindrical leaf to all appearance occupying the apex of a shoot. To clear up this anomaly I investigated the development of the constituent parts of the leaf-bud at various stages of growth, and without going into details which are for this purpose unnecessary, I may say that development supplied the clue which neither outward morphology nor internal anatomy sufficed to give. In point of fact, in the earliest stages examined there were always two foliar tubercles, one of which speedily overpassed the other, so that ultimately all traces of the second leaf were obliterated.

The monophyllous sheath of this pine therefore owes its peculiarity to the generally arrested development of one of its two original leaves.

MAXWELL T. MASTERS, London.

¹ Loc. cit. tab. ix, figs. 5-6.

NOTICE OF BOOK.

DAS GLEITENDE WACHSTHUM BEI DER GEWEBE-BILDUNG DER GEFÄSSPFLANZEN, Von Dr. G. KRABBE. Berlin, 1886.

THE existing investigations on the development of the tissues of plants have dealt rather with the course of the cell-divisions to which the different tissue-systems owe their origin, than with the peculiarities of growth by means of which the elements assume their permanent form. Of late years there has been a tendency, chiefly owing to the influence of Hofmeister and Sachs, to minimise the importance of the single cell, and to regard its growth as subordinate to, and dependent on, that of the whole organ to which it belongs. This view has undoubtedly received support from the recent researches on the continuity of protoplasm through the walls of cells. The brilliant results obtained in this direction by Gardiner, Russow, and others, seem to afford direct anatomical evidence of the mutual dependence of the constituent cells of a tissue 1. A work, therefore, which is entirely devoted to the investigation of those changes in the tissues of plants which are due to the independent growth of their individual cells, claims quite exceptional interest. Such a work is the treatise by Dr. G. Krabbe on sliding growth in the tissue formation of vascular plants.

The object of the present paper is to give a critical account of the more important results of Dr. Krabbe's work on this subject, and to call attention to the conclusions which seem to follow from the facts that he has brought forward.

By the term 'sliding growth' those processes of growth are meant which are accompanied by mutual displacements of certain cells or groups of cells. The fact that changes of this kind occur during the

¹ See especially the introductory passage in Gardiner, Continuity of Protoplasm, in Phil. Trans. Royal Soc., Part iii, 1883, p. 817.

development of the tissues of plants has long been known. For example, the so-called 'false tissues' of most Fungi and some Algae consist of felted masses of interwoven branched filaments arising from a small number of originally distinct hyphae. It is evident that during the growth of such tissues the constituent hyphae must constantly have to force their way between their neighbours, and that thus complicated processes of sliding growth are involved.

A similar case is found in the development of laticiferous cells. These cells, as is well known, attain an enormous length, and send out branches into every part of the plant, so that the whole complex laticiferous system consists of the innumerable ramifications of a small number of undivided cells. The penetration of these branches into the various tissues of the plant necessitates the continual sliding growth of the laticiferous cells on the adjacent cells. As has often been pointed out, these organs behave quite like the hyphae of a parasitic fungus when making their way through the tissues of the host.

Nor has the occurrence of sliding growth in the formation of other kinds of tissue been wholly overlooked. The definition of 'prosenchyma,' for example, even in the older text-books, contains the statement that the end of the cells 'are insinuated into the spaces between those lying above and below them'.' This implies a change in the relative position of the elements in question.

In De Bary's work on the Comparative Anatomy of the Phanerogams and Ferns the occurrence of mutual displacements of cells during their development is explicitly mentioned in various cases. Thus, at p. 462 (English edition) the possibility of such displacements during the formation of irregular groups of sieve-tubes is recognised; and at p. 470 it is stated that the fibrous elements of the wood 'show a great elongation on transition from the cambial condition to that of mature tissue, in the course of which they insert their tapering ends, which are the principal seat of growth, between each other.' Displacements in the transverse direction, due to the growth of large vessels, are also referred to, p. 470.

It would be easy to cite many other passages from the various works on the anatomy of plants, showing that some of the changes comprehended under the term 'sliding growth' have long been known

¹ Henfrey, Elementary Course of Botany, 2nd edition, 1870, p. 501.

to botanists. But, though the existence of phenomena of this kind has been recognised, it will be admitted that Dr. Krabbe is justified in saying that they have never yet been made the subject of accurate study. It is proposed to deal seriatim with the principal points of Dr. Krabbe's work, leaving to the end the more general conclusions suggested by it.

Having defined 'sliding growth,' the author goes on to speak of the cases in which it is well known to occur, pointing out that the most obvious examples, such as those above described in the growth of fungal hyphae and laticiferous cells, are connected with the ramification of cells. He then calls attention to the fact that sliding growth, so far from being limited to cases of this kind, takes place wherever single cells of a tissue grow in such a manner that their original arrangement cannot be maintained. In all such instances there must be independent growth of the several elements of the tissue, resulting in certain definite displacements and changes in their form. These changes are not only remarkable in themselves, but are of interest in relation to the superficial growth of the cell-wall, and also from their influence on the characteristic structure of the various tissues.

The author illustrates the importance of his subject by pointing out that cell-divisions by themselves only play a limited part in the differentiation of the tissues of the vascular plants. The most characteristic constituents of the vascular bundle, namely vessels and sieve-tubes as well as tracheides, and bast and libriform fibres, all owe their mature form to processes of sliding growth. It is further maintained that the differences in the structure of successive annual rings and of spring and autumn wood depend on differences in the individual growth of their cells.

The striking statement is made that whole tissues may be formed by sliding growth, without any cell-divisions taking place; the author here refers, not to the familiar case of laticiferous cells, but to the development of the xylem in the secondary bundles of *Dracaena* and its allies. To this important point we shall have to return. Dr. Krabbe further shows that with the proof of the general occurrence of 'sliding growth' in the higher plants, the distinction between the so-called 'true' and 'false' tissues is obliterated.

The above general considerations serve to define the position of the author, and to introduce his detailed work.

The first part of the subject examined is the sliding growth in the transverse direction, which occurs during the formation of the vessels of the xylem. Attention is chiefly directed to the vessels of the secondary wood of Dicotyledons, as here the regularity of the radial arrangement of the cambial cells and their immediate derivatives renders it comparatively easy to follow the subsequent displacements. In the first instance the growth of the developing vessel in the tangential direction is considered. The author proves that the tangential extension of the cambial zone as a whole, during the development of any one vessel, is so insignificant that it may be left out of consideration.

The exact description of the tangential growth of the young vessels would not be intelligible in all its details without reference to the author's figures. It is shown, however, that the extension which these elements undergo cannot be accounted for in any other way than by the hypothesis of sliding growth between the vessel and the cells of the neighbouring radial rows. Three other possibilities are here discussed; of these only one is sufficiently probable to need mention here, namely, that the vessel in its growth simply compresses and obliterates certain of the adjacent cells. According to Dr. Krabbe's observations such obliteration takes place very rarely, a statement with which those who are familiar with transverse sections of wood will probably agree.

The facts to be accounted for are: that the vessel increases in diameter; that it is in contact with more numerous cells when mature than it was at its first origin, and that the radial rows of cells adjoining the vessel on either side become interrupted by its tangential extension. This penetration of the growing vessel between the adjacent cells is shown by careful measurements to involve sliding growth between the growing portion of the wall of the vessel, on the one hand, and the walls of the cells, between which it penetrates, on the other. In cases where larger vessels are formed this tangential growth may extend through several radial rows. In describing these phenomena the author points out that they cannot be explained without supposing that each cell has a distinct membrance of its own,—a point which does not admit of direct microscopic demonstration at so early a stage.

It is shown that the tangential growth of the vessel is only possible so long as the tissue to which it belongs is undergoing extension in the radial direction, as is actually the case during the development of the young wood from the cambium. Owing to this radial extension of the tissue the growth of the vessel is able to take place without involving the obliteration or even any serious reduction in the dimensions of the neighbouring cells. In this case it is only the tangential extension of the vessel which is due to sliding growth, the increase in its radial diameter being accounted for by the growth of the tissue as a whole. This, however, only applies to vessels of moderate size; the very large vessels, such as are found in the spring wood of the oak, require, as we shall see, sliding growth in the radial direction also for their development.

In connection with this part of the subject the author discusses the interesting question, whether the extension of the vessel is due to growth all round or to localised growth at the points where it penetrates between the neighbouring cells. He decides in favour of the latter alternative. There is nothing improbable in this view, as localised growth often occurs in other cases; at the same time this conclusion cannot be said to rest on any decisive observations.

In the formation of the larger vessels, as already mentioned, sliding growth must take place in the radial, as well as in the tangential direction, for here the radial extension of the vessel is in excess of that of the young wood generally. It is obvious that in this case the growth of the vessels inwards, that is, towards the already formed wood, can only go on so long as the cells in this region are still capable of extension. Towards the cambium the radial growth will be able to go on for a longer time.

Dr. Krabbe next proves that the growth of the vessel may induce sliding between cells not immediately in contact with it. This will be the case wherever the radial growth of the vessel is greater than the average radial growth of the young wood, for here the growth of the cells in the same radial row with the vessel will be less than the average, as the cambium is not displaced. Hence sliding must take place between the slowly growing cells of this radial row (which are passively pushed out by the growth of the vessel) and the cells of the neighbouring rows, which grow at the average rate.

Another case of induced sliding growth occurs wherever the vessel, in its tangential extension, exerts pressure on a medullary ray. The medullary rays are never interrupted by the growth of the vessel, a point of some physiological interest; but they are often, as it were,

bulged out by it. It is shown by the author that the curvature thus induced in the ray causes the cells of the ray to slide on those elements which adjoin it on its convex side.

It is unnecessary to follow Dr. Krabbe in his consideration of the sliding growth of sieve-tubes; the facts are here quite similar to those observed in the development of the xylem vessels.

The cases next dealt with differ essentially from those just described, in so far as the sliding takes place in the longitudinal, instead of in the transverse direction. This occurs in the development of the tracheides, and of the bast and libriform fibres. It is here that the process is most obvious. Where, for example, a fibre of the secondary wood or bast grows to many times the length of the cambial cell from which it is derived, and that at a time when the elongation of the organ as a whole has long ceased, it is clear that mutual displacements must go on between the growing cells. This fact has been insisted on by many observers. The author shows in detail that these displacements necessitate sliding between the growing ends of the cells undergoing elongation. He further points out, that the process can only take place in a tissue which is still growing in the transverse direction. The tracheides or fibres insert their ends between cells, which are at first in contact with one another, and thus additional room is required, which can only be afforded by general transverse growth of the tissue. Dr. Krabbe shows that the small cell-lumina, which are found in transverse sections between the larger elements, represent the cut ends of intruding prosenchymatous cells. All elements, which thus force their way between those lying above and below them, must necessarily undergo changes of form in this process.

It would have added to the interest of this part of the work if the author had been able to add figures of the fibrous elements at intermediate stages of their development from the comparatively short cells of the cambium. This would have given a much clearer idea of the phenomena actually involved than can be attained by the aid of reasoning alone.

Although the occurrence of sliding growth is most evident in the case of the secondary tracheides and fibres, which are developed in regions no longer undergoing general elongation, there is no reason to doubt, that the same process goes on during the formation of the primary tissues. The author points out, that the disturbances actually

observed in the arrangement of the cells afford evidence for this. Careful comparative measurements, both of the growth of the whole organ and of the individual fibrous elements, are clearly necessary in all such cases.

Dr. Krabbe then proceeds to discuss the development of the xylem in the secondary bundles of those Monocotyledons which are capable of indefinite growth in thickness. These bundles are formed from the cambium in parts of the stem in which longitudinal growth has ceased. Dracaena Draco is the first example considered. In most cases all the elements of a bundle seen in any transverse section arise from a single cell of the cambium. The bundles are here concentric, the small phloëm being surrounded on all sides by the xylem. latter contains some woody parenchyma, but is chiefly composed of very long tracheides. The formation of a new bundle begins with the appearance of longitudinal divisions in a cell of the cambial zone. The cells thus formed only differ from the cambial cells in their smaller diameter and in their transverse walls becoming slightly inclined instead of horizontal. These young elements of the vascular bundle may be termed, for the sake of clearness, the sub-cambial cells. Now the length of these cells, which is very constant, is found by Dr. Krabbe to average o.1 mm. The average length of the mature tracheide is 3.8 mm. Thus, as each sub-cambial cell, which becomes a tracheide, grows to thirty-eight times its original length, while there is no elongation of the organ as a whole, it follows that in any given transverse section the mature tracheides cut through will appear on the average thirty-eight times as numerous as they would have appeared before their elongation. Or, in other words, each mature tracheide will make its appearance in successive transverse sections thirty-eight times as often as the sub-cambial cell from which it is derived. The author has repeatedly counted the tracheides seen in a transverse section of a fully formed bundle. He finds that their number varies from thirty-two to forty-four, the mean thus being thirty-eight. On the author's assumptions it is possible to calculate from these data the number of sub-cambial cells at any one level, which give rise to the tracheides. It may be convenient to give a general expression for his calculation, as it is applicable to all cases of longitu-

¹ This is not the terminology used by the author, but the terms adopted here will probably be more intelligible to English readers.

dinal sliding growth, if branching of the cells be left out of consideration. If the total number of mature tracheides seen in a transverse section be called x, the number of sub-cambial cells from which they are derived will be $\frac{x}{m}$, where m is the ratio of the length of the mature tracheide to that of the sub-cambial cell. In Dracaena Draco the average value of x is thirty-eight, and that of m is also thirty-eight. Hence the number of sub-cambial cells at one level, which become tracheides, will be one, i.e. the whole system of tracheides in each bundle arises from a single vertical row of sub-cambial cells. Here then, according to Dr. Krabbe, we have a most striking case of the formation of a system of tissue from a simple row of cells, without the aid of any further cell-division. The tracheides form by far the most important constituent of the bundle, and the author estimates that fourteen-fifteenths of the whole sectional area of the bundle are occupied by tissues developed by sliding growth. Thus, on this hypothesis the central phloëm must gradually become enveloped by the growing tracheides, as by a web of hyphae. It is unnecessary to enter into a more detailed consideration of this case or of the similar phenomenon alleged to occur in Aloe and Yucca. It will be well known to many readers, that a totally different explanation of the development of the so-called tracheides of these plants has been given by Professor Kny¹, in a work published almost simultaneously with that of Dr. Krabbe. Professor Kny finds that the elements in question are not tracheides at all, but short vessels, arising from the fusions of a series of sub-cambial cells. If this be the case, their formation does not necessarily involve sliding growth, though Professor Kny allows that this may occur to a small extent at the ends of the elements.

So direct a contradiction in the results obtained by two competent observers is certainly remarkable, and further investigation is urgently required. The writer of this article has himself made some observations on this subject, but they are not yet sufficiently complete for publication. The very pointed ends and occasional branching of the tracheides indicate that a certain amount of sliding growth must take place, but this by no means excludes the possible occurrence of cell-fusions.

¹ Beitrag zur Entwickelungsgeschichte der 'Tracheiden.' Berichte der deutschen bot. Gesellschaft. Bd. IV, S. 267, 1886.

The remainder of Dr. Krabbe's work, though touching on many points of great interest, will not require detailed consideration.

Some of the points here discussed, as, for example, the causes of annual rings and the relation of turgidity to growth, have only an indirect connection with the immediate subject of the paper.

In my opinion it must be granted that Dr. Krabbe has succeeded, not only in demonstrating the occurrence of sliding growth, but in showing that it is probably universal among vascular plants, and that thus the difference between their tissues and the false tissues of the Fungi and Algae is only a difference of degree. Special cases, like that of *Dracaena* and its allies, will clearly require much further investigation, and in all cases of longitudinal sliding growth there is room for additional evidence from direct observations of the elements at various stages of development.

In the light of the author's researches it is clear, that greater importance must be attached to the independent growth of the individual cell than has been usual in recent years. The structure of the most important tissues depends to a great extent on the special mode of growth of certain of the constituent cells.

The fact that sliding growth takes place between very young cells is also of interest as proving that the wall between them must be a double one, even at this early stage. This conclusion agrees with the observations of Wiesner¹.

The localised growth of certain portions of the cell-wall is no new discovery, but Dr. Krabbe's observations supply additional instances of its occurrence. It is probable that the careful study of cases of this kind will confirm the author's conclusion, that the turgidity of the cell is by itself quite insufficient to account for the phenomena of growth.

Dr. Krabbe is of opinion that continuity of the protoplasm through the cell-wall cannot exist in the case of any cells between which sliding growth takes place. In this I am unable to follow him. It is well known that the perforation of the sieve-plates is a secondary process, the plate at its first origin being a continuous cellulose wall. It appears quite possible that the same may be true of the more delicate perforations through which the protoplasm is continuous

¹ Untersuchungen über die Organisation der vegetabilischen Zellhaut. Sitzungsberichte der Kais. Akad. der Wissenschaft. Wien, 1886.

from cell to cell, and if this be so there is no reason why the pores should not be formed after the sliding growth is completed. It is certain that vessels and other elements with sliding growth have corresponding pits. These pits must be developed when the mutual displacements are at an end, and it is quite likely that the perforation of their closing membranes may take place at the same time. We must wait for further researches on the development of the protoplasmic strands in the cell-wall before this point can be determined. It is of interest to note that, according to the researches of Fischer¹, the sieve-tubes are connected by fine protoplasmic strands, not only with one another, but also with their companion cells; but that neither of them are connected with the cambiform cells. The latter, however, are in communication among themselves. It would be important to ascertain whether these differences have any relation to the sliding growth of the various elements on one another.

It may be hoped that Dr. Krabbe's work will lead to much important investigation along the lines which he has indicated.

D. H. S.

¹ Neue Beiträge z. Kenntniss d. Siebröhren, Berlin, Gesellschaft Wiss. 1886.

Arceuthobium Oxycedri.

BY

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With Plate X. A.

O much has already been written on this genus of the Loranthaceae that many readers of the Annals will no doubt be surprised that there should be anything new to be said on the subject. Indeed I intended at the outset of this investigation to confine my remarks to the mechanism of dehiscence of the fruit, but an examination of the plant led me further, especially as the published accounts of the plant differ from my own observations in some important particulars. I suppose the reader to be acquainted with the characters of the plant, of which a technical description, extracted from the Genera Plantarum of Bentham and Hooker, will be found on the next page. This paper begins with a description of the contents of the ovary as seen by myself, followed by its comparison with the observations of different investigators of the characters of Arceuthobium and other Achlamydospermeae; after which the endeavour is made to assign to the structures in the ovary their morphological values. Descriptions of the structure of the fruit and, as a result, of its peculiar mode of dehiscence follow naturally. The arrangement of the parts of the expanded male flower as seen under the compound microscope, succeeded by the development of the male flower and of an individual stamen, is next taken, the last parts of the plant considered being the vegetative organs, already fully

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examined by Solms-Laubach. A summary of the investigation as a whole is given at the end of the paper. My knowledge of the plant is limited to spirit and herbarium material, all the figures being derived from spirit specimens of the plant, for which my thanks are due to Dr. Scott, to whom the material was given by Mr. Thiselton Dyer.

Arceuthobium¹, Bieb. Fl. Taur. Cauc. Suppl. 629 (Rasoumowskia, Hoffm. ex Bieb. l. c.).

Flores dioici, in axillis solitarii. Perianthii tubus in fl. 3 2-5 partitus, in fl. 9 minimus, 2-partitus. Antherae fl. 5 in medio segmentorum sessiles, transversae, loculis confluentibus rima unica dehiscentibus, demum apertae fere orbiculares. Discus utriusque sexus carnosus. Ovarium fl. 9 ovoideum, ad normam ordinis sante fecundationem solidum apparet v. in centro textura tenuiore plus minus distincte (in speciminibus siccis) cavum, ovulo saepissime a substantia ovarii non rite distinguendum, etsi a variis auctoribus nunc erectum nunc pendulum v. lateraliter affixum dicitur.] (v. ex Baillon ovulo distincto v. basi erecto); stylus brevis, crassus, subconicus, stigmate obtuso. Bacca ovoidea, breviter stipitata, perianthii lobis minutis coronata, basi lata ad apicem dilatatam stipitis adnata, pericarpio carnoso viscifluo, endocarpio sæpe distincto, maturitate basi circumscissa et elastice dehiscens, semen longe ejiciens. Semen ovoideo-oblongum; embryo albumine carnoso copioso inclusus. Fruticuli in arboribus imprimis coniferis parasitici, subaphylli, foliis nempe omnibus ad squamas parvas oppositas in vaginam apertam coalitas reductis. Flores in vagina utrinque solitarii, parvi, sessiles v. subsessiles, ebracteolati.

Species 5 v. 6, quarum una per Europam australem, Asiam occidentalem, et Americam boreali-occidentalem late dispersa, caeterae Americae borealis imprimis occidentalis v. Mexici incolae.

On making longitudinal sections of a female flower of Arceuthobium Oxycedri at a stage corresponding to pollination (end

¹ G. Bentham and J. D. Hooker, Genera Plantarum, vol. iii (1883), p. 213.

of September or beginning of October) and in such a direction as to pass through the median plane of the two perianth-segments, the unilocular inferior ovary will be seen to be almost entirely filled by a conical cellular papilla continuous with the cells forming the floor of the ovary and projecting freely into the ovarian cavity. On the surface of the cone lie the distinctly columnar cells of the continuous epidermis and beneath it is a mass of cellular tissue, near the apex of which two large ovoid cells occur, one towards each side of the axis of the papilla, and having their outer sides parallel and in contact with the epidermis (Fig. 1). These are two embryosacs, and they are obliquely inclined towards one another, and only separated at their upper, usually broader ends by one or two median cells of the papilla.

Each embryo-sac has a thick highly refractive pitted cellulose wall enclosing very abundant and granular protoplasm. In a successful preparation the arrangement of the cells in the interior of this embryo-sac may be ascertained, as shown in Figure 2.

Though I was not able to see all the stages from the uninucleate condition to that in which the embryo-sac is ready for fertilisation, I saw enough to convince me that the development is as in a normal Angiosperm. In one embryo-sac there was at the antipodal end a resting nucleus and one in the segmentation stage, in another there were two nuclei meeting in the middle of the embryo-sac, and other intermediate stages were observed. The antipodal cells of the embryo-sac were in all cases quite distinct; but it was different with the egg-apparatus. Both synergidal cells and oosphere were often so obscure that their presence could not be ascertained with certainty. This negative result may have been due partly to the exceeding granularity and tendency to opacity of the general protoplasm, and partly to the faintness of the nuclei themselves, a phenomenon which has been observed in other parasites1. In several cases however,

¹ Hofmeister records this of *Viscum album*. This is the more strange since the nuclei in the other parts of parasites are usually so distinct.

especially after staining with saffranin or picronigrosin, the two apical synergidal cells and the lateral oosphere were distinctly seen. The general outline of the ovarian papilla is not affected by the presence of the embryo-sacs; there is no indication by lobes on the papilla of their occurrence in its interior.

Each embryo-sac arises as a hypodermal cell which divides by a horizontal wall into two; the upper and smaller cell is the primary tapetum-cell, and divides into two by a vertical wall. The lower one is the mother-cell of the embryo-sac, and after having cut off from its lower end two small cells by horizontal walls, it enlarges into the embryo-sac. The nucleus of the uninucleate stage of the embryo-sac is very large and pronounced (Figs. 4–5). Whether each embryo-sac should be regarded as derived from a special hypodermal archesporium, or as a fully developed cell of a hypodermal multicellular archesporium common to the two embryo-sacs, will be made clear, it is hoped, by what is said further on.

The flowers were seen first in September, by Reinaud. Pollination occurs towards the end of September or the beginning of October, and judging from analogy with Viscum album and Loranthus europaeus, fertilisation does not take place till the following spring. The thin pollentube passes down the stylar canal and penetrates into the ovarian papilla at its summit, passing into it for a certain distance towards the apex of the embryo-sac and resting there till the beginning of vegetation in the next year. It seemed, on first consideration, that the interval of time between pollination and fertilisation gave some support to the suggestion of Marshall Ward¹ that the effect of parasitism is to degrade sexual organs and their function; that, indeed, there might be some subtle connection between fertilisation and the formation of the seeds in parasite and host in the case of Arceuthobium, which grows on Pinus2 or on Juniperus, the two genera of the Coniferae in which a year intervenes between

¹ Marshall Ward, in Q. J. M. S. xxiv.

² Pinus brachyptera, P. Banksiana, Juniperus communis, J. Oxycedrus.

pollination and fertilisation. The occurrence, however, of a similar long interval in *Viscum album* growing on the apple which shows no such interval does not give much countenance to this view.

Before attempting to assign to the ovarian papilla and its two embryo-sacs their morphological values it will be well to consider the condition of the ovary as seen in *Arceuthobium* and other Loranthaceae (Eulorantheae and Visceae of the Genera Plantarum) by different observers.

1. Arceuthobium.

Professor Oliver was the first, in 1870, to notice a papilla in the ovary of Arceuthobium, the species being A. cryptopodum. I cannot do better than quote his remarks:- From the material at my disposal I cannot at present satisfactorily explain the nature of the ovuliform body. It may be a fertilised embryo-sac the lower portion of which is so engaged in its early stage in the subjacent cellular tissue as to appear to be in continuous connection with it. In this case the minute enclosed sac bounded by a free but well-defined membranous wall and full of more or less distinct definite cells must represent an early condition of development of the embryo in the embryo-vesicle, although its occurrence thus, as a minute spherical sac without trace of suspensor near the apex of an embryo-sac already filled with cellular tissue, appears to be at variance with the usual mode of its formation in Loranthaceae.

'On the other hand, the papilla [figures 8 and 9 in Icones] looks at first sight much like a naked free ovule, and the enclosed vesicle [figure 10 in Icones] an embryo-sac filled with cellular tissue. Against this apparently reasonable view is the circumstance that at the stage represented by figure 9 [in the Icones], or rather later, the entire body exhibits a tendency to separate on pressure by a clear line at the base from the tissue beneath. We have not, moreover, any case that I am aware of in Loranthaceae, in which the ovule is wholly free.

¹ D. Oliver, in Hooker's Icones Plantarum, 1870, t. 1037.

'I recommend the case to those botanists who may happen to have access to a sufficient series of specimens in different stages of development.'

In 1876 Baillon¹, admittedly owing to Professor Oliver's description, examined Arceuthobium Oxycedri in many stages of its development. At one stage he found a freely projecting basally attached cellular papilla in the ovary, which he described as an ovule naked and orthotropous and comparable to the nucellus of Polygonum. All the cells of this 'ovule' in its free condition and when pollination has taken place are represented as uniform; it is not until later, when the ovule is no longer free but is enclosed in well-developed viscid cells [which are not formed in Loranthaceae until after fertilisation, that one embryo-sac, median and apical, is said to be formed and fertilisation to occur. It will be seen how different this account is from that which I have given above. M. Baillon seems to have overlooked the embryo-sacs. A comparison of the figures in Plate VI. of the Association Française, 1876, shows that the embryo-sac s has the same relation to o the young seed in fig. 17 that the embryo e has to the endosperm (unnamed) in figures 19 and 20. I believe all three figures represent very similar stages in the development of the fruit, and prefer to think the lettering s the embryo-sac in fig. 17 a slip of the pen for e the embryo, rather than to suppose that the embryo-sacs have been overlooked and the embryo mistaken for one of them. Some years before, in 1840, Sir W. J. Hooker 2 took Arceuthobium as the type of the Loranthaceae, and for the first time figured the male and female flowers of Arceuthobium, making use of A. Oxycedri for the purpose. In Tab. XCIX. fig. 8 of the Flora Borealis Americana an undissected female flower is represented. It looks however very much like a young fruit, and the likeness is still more apparent in fig. 9, which is a longitudinal section of the same. There is no ovarian

² W. J. Hooker, Fl. Bor. Amer., 1840, t. 99.

¹ Baillon, Fleur femelle de l'Arceuthobium Oxycedri, in Assoc Franc. Clerm., 1876, p. 495, t. 6.

cavity present, and the apical central sac shown nearly enclosed in cellular tissue is not the embryo-sac but the embryo imbedded in endosperm, as is the case in fig. 12 of the same Plate.

2. THE OVARIAN PAPILLA IN OTHER LORANTHACEAE.

In 1836 Griffith's valuable and interesting paper, 'Notes on the Development of the Ovule of Loranthus and Viscum,' appeared. In Viscum [species not given] he found a nipple-shaped process in the ovarian cavity, at the base of which he saw two projecting more or less pendulous bodies, which he regarded as naked ovules, the nipple-shaped process being the placenta. This arrangement was so different from anything seen in any genus of the Loranthaceae, more especially so different from what several subsequent observers saw in species of Viscum, and at the same time so like the condition of the gynaeceum in the Santalaceae (e.g. Santalum album as described by Griffith's himself), that by Hofmeister and others Griffith's Viscum was regarded as a genus of the Santalaceae. Against this, however, Treub has protested, for he considers our knowledge of the structure of the gynaeceum of the Loranthaceae too imperfect to permit of dogmatism, and his protest is supported by the structure of A. Oxycedri. It is not difficult to see how the two apical embryo-sacs buried in the nipple-shaped process in A. Oxycedri could be derived from the two basal pendulous projecting bodies on the nippleshaped process in Griffith's Viscum. In Griffith's Loranthus Scurrula neither ovarian cavity nor papilla was seen. a later paper—read 1843—Griffith³ describes a Malaccan Viscum in which he found no nipple-shaped process, but such a process was found in Loranthus bicolor, though in it subsequently rendered obscure by the migration of the embryosacs half way up the style.

¹ Griffith, in Trans. Linn. Soc., xviii. p. 76.

² Griffith, in Trans. Linn. Soc., xviii. p. 59.

³ Griffith, in Trans. Linn. Soc., xix.

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In 1858 Hofmeister¹ described an ovarian cellular papilla in *Loranthus europaeus* and in *Viscum album*. In each case he found the papilla lost its identity at an early stage by fusion with the surrounding tissue, the ovarian cavity becoming obliterated in the process.

In 1859 Hofmeister² entered into much more detail as regards these two plants, and from his illustrations it is apparent that the ovarian papilla is far less pronounced in either plant than in *A. Oxycedri*. A whorl of three (often only two) embryo-sacs was observed, their position relatively to the carpels not being given.

Of *Viscum album* Hofmeister says, 'The carpels soon come into contact with one another by their upper flattened surfaces, leaving only a narrow intervening space. The group of very few cells at the bottom of this space must be regarded as the ovule of the mistletoe³.' Two to three embryo-sacs were found in a later stage, formed from cells beneath the, now, absent ovary.

Hofmeister described a third form of the Loranthaceae, Lepidoceras Kingii⁴, in which he saw a long free much attenuated ovarian papilla having some three embryo-sacs in it at its base.

In 1869 Van Tieghem⁵ found it impossible, after repeated attempts, to observe any ovarian papilla in *Viscum album*, and came to the conclusion that it does not exist. Several embryo-sacs were found formed from sub-epidermal cells of the upper (ventral) surfaces of the carpels in their median plane. If more than one embryo-sac was formed for each carpel, they were still in its median plane and one above the other. Unfortunately the descriptions are not illustrated.

¹ W. Hofmeister, Neuere Beobachtungen über Embryobildung der Phanerogamen, in Pringsheim's Jahrbücher, i. 1858, p. 113.

² W. Hofmeister, Neue Beiträge zur Kennt. d. Embryobildung d. Phanerog. in Abh. der Sachs. Ges. d. Wiss., vi. 1859, p. 634, Plates I-IX.

<sup>W. Hofmeister, op. cit. p. 555.
W. Hofmeister, op. cit. p. 552.</sup>

⁵ Van Tieghem, Anatomie des fleurs et du fruit du Gui, in Ann. Sc. Nat. xii. p. 101.

In 1881 Treub¹ began his 'Observations sur les Loranthacées,' the first species described being Loranthus sphaerocarpus. In this he found an ovarian papilla with several apico-lateral slightly projecting lobes on it. This papilla, like that found by Hofmeister in Loranthus europaeus, soon fuses with the surrounding tissue, causing the gynaeceum to appear in section as a solid body composed of vertical continuous columns of cells, each originally distinct lobe of the papilla being now represented by an elongating embryo-sac. In forms still more recently examined, Viscum articulatum² and Loranthus pentandrus³, Treub found no ovarian papilla, though in the last-mentioned species there was a slight indication of a tendency to form one.

3. MORPHOLOGICAL VALUE OF THE OVARIAN PAPILLA AND ACCOMPANYING STRUCTURES IN LORANTHACEAE.

Griffith purposely called the papilla in *Viscum* and in *Loranthus bicolor* a nipple-shaped process in order to leave open the question of its morphological nature. He would go no further than to say he regarded this process as a placenta, and the two projections on it in *Viscum* as naked ovules. He regarded the condition in the Loranthaceae as an extreme reduction of the free central placenta with ovules of such an angiosperm as *Primula*, an intermediate stage being exhibited by the Santalaceae.

Hofmeister regards the papilla in the plants in which he found it as a free naked orthotropous ovule containing several fully developed embryo-sacs.

Professor Oliver's opinion as to the nature of the papilla in *Arceuthobium cryptopodum* has been already quoted (ante, p. 141).

Baillon says of A. Oxycedri, 'The papilla is an ovule, erect, orthotropous, and comparable to the nucellus of Poly-

¹ Treub, in Annales du Jardin Buitenzorg, ii. 1^{1èm} partie, p. 54, Plates VIII-XV.

² Treub, in Annales du Jardin Buitenzorg, iii. 1^{ième} partie, p. 1, Plates I-II.
³ Treub, in Annales du Jardin Buitenzorg, iii. 2^{ième} partie, p. 184, Plates XXVIII-XXIX.

gonum' [and like it formed of the modified apex of the floral axis 1].

Treub cannot think that the ovarian papilla in Loranthus sphaerocarpus is an ovule; the hypothesis which he suggests is this 2: 'La région axile du mamelon, constitue un placenta, et les trois ou quatre segments latéraux libres, qui se produisent, sont des ovules rudimentaires. La pluralité des cellules-mères de sacs embryonnaires, dans chaque segment empêche d'assigner le rang d'ovules aux sacs embryonnaires mêmes.' In support of this hypothesis Treub found the ovules (usually four) in Loranthus sphærocarpus represented by distinct lobes near the apex of the placenta. In each lobe there was a large number of embryo-sac mother-cells side by side, of which only one gave a fertilisable embryo-sac.

There are no lobes on the papilla in A. Oxycedri. The two embryo-sacs are separated by uniform tissue, each one is apparently derived from a unicellular hypodermal archesporium, and so in this respect there could be no objection to regard each embryo-sac as an ovule. It would not be a long step from Loranthus sphaerocarpus to A. Oxycedri, thus passing to a placenta bearing two completely imbedded ovules reduced in each to a single archesporium cell.

Several objections may be urged to the view that the papilla in A. Oxycedri is an erect orthotropous ovule containing two fully developed embryo-sacs. There is no example in the Phanerogams of an ovule containing two such embryo-sacs. It would be a forced comparision to regard the condition in A. Oxycedri as capable of explanation by reference to the macrosporangium of Isoëtes. The nearest approach to this structure of an ovule is that described by Strasburger for the ovule of Rosa livida³. In this plant there is a multicellular archesporium forming (generally) four embryo-sac mother-cells lying side by side. Of these only one, after they have all passed through one or

3 Strasburger, op. cit., p. 14.

Strasburger, Die Angiospermen u. d. Gymnospermen, p. 3.
 Treub, in Annales du Jard. Buitenzorg, ii. p. 64.

two division-stages, gives a mature embryo-sac. If we think of the papilla in A. Oxycedri as an ovule, we have an archesporium which is apical, hypodermal and multicellular, from which two embryo-sac mother-cells develope into ripe embryosacs, the cells between them being undeveloped sporogenous tissue. If this view be correct, we have in this parasite an ovule which is more highly developed than in any other Phanerogam. It would too be quite opposed to the basis of the distinction of the Loranthaceae from the Santalaceae. The absence of a distinct ovule in the Loranthaceae is the essential ordinal character of separation from the Santalaceae. regard the papilla in A. Oxycedri as an ovule would be to give to the most modified genus of the Loranthaceae a structure on the absence of which the separation of the Loranthaceae from the Santalaceae is based. It appears to me to be impossible to regard it as an ovule, and yet, as in the case of Myzodendron, to exclude it from Santalaceae.

I hoped that a consideration of the relative time at which the papilla in the different Loranthaceae appears would throw some light on its morphological value. Hofmeister in Loranthus europaeus and in Viscum album, and Treub in Loranthus sphaerocarpus, found that the ovarian papilla appeared after the carpels as an upgrowth from the floor of the ovary; and of L. sphaerocarpus it is recorded that the segments appear later, followed by the formation in their interior of their respective embryo-sacs. Whether the placenta in L. sphaerocarpus should be regarded as formed by the fusion of 'claws' of the carpels, as in Santalum album and Primulaceae, or as a derivative of the apical part of the floral axis, does not appear.

The time of appearance of the papilla is different in A. Oxycedri. Baillon found that the apical part of the floral axis persisted throughout the development of the female flower, changing from a hemispherical to a conical swelling in becoming the ovule. It should however be mentioned that the embryo-sacs were overlooked. While in the case of this plant a knowledge of the time and mode of development of

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the papilla does not help one to decide its whole nature, it does prove that it is a modified part of the floral axis and not a body derived from the fusion of the 'claws' of the two carpels. The definiteness of position of the two embryo-sacs in A. Oxycedri should be taken into account. After cutting longitudinally a number of pollinated flowers without getting satisfactory views of the embryo-sacs except as it seemed accidentally, I found by making longitudinal sections through the median plane of the two perianth-segments that I almost invariably got complete sections of the two embryo-sacs. I also made successive transverse sections of the flower, beginning in some cases at the apex of the style, in others at the base of the flower. I had noticed that the apex of the style was grooved, that the stigma was bilobed, and that the lobes were elongated parallel to the upper (ventral) faces of the perianth segments. The sections showed—

- 1. That the style was traversed by a canal formed by the unapplied parts of the ventral faces of the carpels.
- 2. That this stylar canal was, as seen in transverse section, elongated parallel to the ventral faces of the carpel (Fig. 7).
- 3. That there were two embryo-sacs opposite the median planes of the two carpels (Fig. 6).
 - 4. That the carpels had no vascular bundles.
- 5. That the carpels were *opposite* the two segments of the perianth (Fig. 7).

It was not without much hesitation that I allowed myself to be convinced that the carpels are evascular and opposite the perianth-segments, for by Eichler¹ and Baillon² they are placed at right angles to the lobes of the perianth (compare Figs. 1, 6 and 7 with Fig. 236 in Blüthendiagramme). It should be stated that in a few cases isolated irregularly distributed (reticulate), isodiametric tracheides were found in the carpels. Taking all the different circumstances into account, I prefer, so far as I may express an opinion, to follow the direction of Treub's view of Loranthus sphaerocarpus, and to call the ovarian papilla in

¹ Eichler, Blüthendiagramme, p. 553. ² Baillon, op. cit on p. 142, Plate VI.

A. Oxycedri a placenta formed of the modified apical part of the floral axis bearing two imbedded ovules reduced to their simplest condition, that of unicellular hypodermal archesporia, one mature embryo-sac being developed from each of the two archesporial cells.

4. THE FRUIT OF A. OXYCEDRI.

It is known that an interval of fourteen months elapses between the formation of the female flower and its dehiscence as a ripe fruit. Unfortunately, the material at my disposal was collected at one time, probably the middle of November. Mr. Carruthers very kindly gave me some dried material of A. Oxycedri from the Herbarium of the Natural History Museum; it was unfortunately in the same stages as my spirit material, as was also some in the Herbarium at Kew which Professor Oliver was so good as to look through with me. It was so well preserved that nearly all the details seen in the spirit material could be verified in it.

Between the oldest pollinated flower and the youngest fruit there is a difference of a year. I cannot say whether Arceuthobium shows any migration of its embryo-sacs or embryo such as Griffith, Hofmeister, and Treub have seen in different Santalaceae and Loranthaceae. It would be still more interesting to know whether the two embryo-sacs have each an embryo and endosperm, whether the two sacs become ever fused, whether if there are two endosperms they become one; phenomena observed by Van Tieghem in Viscum album. There is one important respect in which the reduction in Arceuthobium is much less than in other Loranthaceae. While in other Loranthaceae the papilla of the ovary when present becomes fused with the wall of the ovary so that the gynaeceum is a solid body even before fertilisation, this does not happen in Arceuthobium. The ovarian papilla does not at any time become fused with the wall of the ovary.

In the ripe fruit the apical part of the papilla forms a sort of calyptra to the radicle, and the basal part is thrust to one

side by the enlarging endosperm, beneath the base of which it is visible as a yellowish patch of completely crushed cells, the walls of which are not easily made out. Reinaud's 1 is the only account I have found of the dehiscence of the fruit, and to his description I must acknowledge my indebtedness in framing the explanation of the dehiscence I have suggested at the end of the description of the fruit. Unfortunately, Reinaud's paper is not illustrated. He found the parasite growing equally well on Funiperus Oxycedri and F. communis in the woods of Sisteron. The female flowers are visible in September, and ripe fruits in November of the following year, by the end of which month they are all fallen. says of the fruit, 'It is a little more than two millimetres long, and not quite one millimetre broad. The lower part up to just beyond the middle is cylindrical, smooth, transparent, and of a pale yellowish green colour. longitudinal and diametrically opposite lines, the rudiments of the commissures, are visible through the transparent wall [the two vascular bundles of the perianth]. The seed is embedded almost entirely in this part in the midst of a colourless liquid. The upper cap-like part of the fruit is pulpy, opaque, greener, and conical. The fruit is detached from the plant at its articulation with the peduncle, by which operation a circular hole is formed. This dehiscence takes place suddenly with elasticity, the seed is forcibly ejected through the resulting opening by the help of the liquid in which it is found, and by which the pressure of the pericarp is communicated to it. In this way the seed is thrown more than a metre, carrying with it the viscid part of the "umbilical cord." It is mentioned that the dehiscence of the fruit in Momordica Elaterium is very similar (I have been struck quite sharply with its ejected seeds standing two and three yards off).'

Before attempting an explanation of the dehiscence I will supplement this description of macroscopic features of the

¹ M. Am. Reinaud de Fonvert, Note sur *L'Arceuthobium Oxycedri*, in Annales des Scien. Nat., 3° série, T. vi (1846), p. 130.

fruit by an account of the microscopic structure. In a vertical median section of a ripe fruit (Fig. 8) the centre is seen to be occupied by ordinary endosperm tissue of large volume and with a single median embryo imbedded in its apical part (Fig. 9). I have never found more than one embryo. It is straight, with the two cotyledons only very slightly indicated. Its radicle is superior and has no root-cap; the whole embryo is covered by a continuous layer of columnar dermatogencells (Fig. 10): the radicle is exserted; the endosperm-cells extend no further upwards than to the point at which the hypocotyledonary stem passes into the radicle. The protective function of the root-cap is apparently assumed by the apical part of the ovarian papilla which forms a conical cap of empty cells covering the radicle much as the calvptra of the Moss covers the tip of the developing sporogonium. The absence of a true root-cap and the faint indication of the cotyledons are characters in keeping with the parasitic habits of the plant, and are conspicuous in other parasites, e.g. Cuscuta¹. The only differentiated part of the embryo is the epidermis; the sub-epidermal tissue is uniform, and there are no procambial strands.

Owing to the absence of the integument of the ovule, and consequently of the testa of the seed, the protective function of the testa is assumed by the endocarp, which forms a complete envelope to the seed when the latter is forcibly ejected from the dehisced fruit. The endocarp consists of some five layers of cells. All the layers except one, and this the outermost, consist of simple thick-walled cells without contents, parenchymatous at the apex and base, prosenchymatous laterally. The outermost layer is, except in its basal part, converted into obliquely radiating viscid cells, some of which are half the length of the seed proper, their length as a general rule being greater the nearer they are to the radicular end of the seed. The walls of

¹ Goebel, Vergl. Entwick. d. Pflanz.; Anhang, Parasiten, in Schenk's Handbuch der Botanik, 1884, p. 374.

the viscid cells have become converted into viscine, and, in spirit-material, are as broad as the lumina of the cells. In many, by no means all, viscid cells the wall presents thickening in the form of a double spiral. I have seen side by side in different cells a double spiral, a single spiral, and annular markings. When fully developed the cavities of the cells have each a very thin layer of parietal protoplasm enclosing a large quantity of cell-sap. At each end the cavities of the cells are dilated (Fig. 12). On its inner surface this outermost layer is organically continuous with the rest of the endocarp, while at its outer surface it is just as intimately connected with the mesocarp, though the connection is less easily made out.

I have given this detailed description of the endocarp, since the origin Baillon assigns to the viscid cells is essentially different and at variance with what is known of their derivation in other fruits:- The surface of the ovule presents interesting changes which render the internal appearance of the ovule and fruit quite different. The most external cells of the ovule grow rapidly and produce projecting papillæ on the originally naked surface of the nucellus. These cells soon become long viscid hairs which fill the cavity of the pericarp and have a double spiral on their walls. In the end all these soft and viscid hairs lie close together and form a kind of pulp which could be taken for a continuous parenchyma. It is the nucellus which here provides the integumentary covering, it is from it also that the internal parenchymatous mass playing the part of the endosperm is derived 1.' Striking proof of the incorrectness of this view came in quite an unexpected manner. material I had received from Mr. Carruthers were several very young fruits, judging from their size. On making sections the cause of their smallness was plain. There was no seed at all formed; the ovarian papilla had died early, and though readily recognisable was shrivelled; nevertheless the

¹ Baillon, op. cit. on page 142, p. 500.

pericarp had passed through most of the changes seen in it in a ripe fruit; the viscid cells were comparatively well-developed; and yet between the inner surface of the endocarp, of which the viscid cells were the outer surface, and the shrivelled ovarian papilla ('nucellus' of Baillon) there was a large gap of the same nature as that in the ripe fruit between the endocarp and the endosperm. It was of interest to find all the specialised accessory modifications in the fruit, while the essential parts, embryo and endosperm, were quite absent.

Returning to the ripe fruit, the mesocarp consists of two strata, an inner one composed of thin-walled cells pressed completely out of shape, and an outer one, which, between the points a and b in Fig. 9, consists of five or six layers of thick-walled pitted parenchymatous cells. The walls are lignified and the pits wide (Fig. 11). The change from this sclerotic tissue to thinwalled cells above b and below a in Fig. 9 is very abrupt. At a, Fig. 11, represented on the surface of the fruit by a circular horizontal groove (the place of articulation of the fruit with its peduncle), there is, as seen in a longitudinal section, a horizontal plate of extremely thin-walled cells, eight to ten tiers high, and formed very probably by the meristematic activity of a single layer of cells. Where this meristematic tissue abuts against the vascular bundles the xylem vessels atrophy. Between its uppermost layer and the base of the endosperm the lower part of the 'endocarp,' some five layers thick, is situated. At dehiscence of the fruit this zone of meristematic tissue is torn in two horizontally, the vascular bundles being also transversely cleft. (Cp. Fall of Leaf1.) Taking these structural facts into consideration, it seems to me an anatomical explanation of the mechanism of dehiscence of the fruit may be given. Before fertilisation the unoccupied part of the ovary is very small, the ovarian papilla is almost in contact with the wall of the ovary. This is not less so after fertilisation. The formation of the bulky endosperm begins simultaneously with intercalary divisions of the pericarp.

¹ Strasburger, Bot. Pract., 1887, p. 223.

This latter process does not keep pace with the former; the basal part of the ovarian papilla is pressed out of shape by the developing seed, which is also causing considerable pressure on the pericarp, so much so that the inner part of the mesocarp is completely crushed, an obliteration which does not extend to the outer part of the mesocarp, the walls here having begun to be thickened and lignified. The seed comes to have a relation to the pericarp similar to that of the protoplasm to a cell-wall in a turgid cell. The mutually exerted pressure is further and greatly increased by the formation of the thick layer of viscid cells, a formation which has proceeded with the other changes in the production of the fruit. maturity the degree of tension is so great, the weakest part of the pericarp gives way. This spot has already been prepared by the development of the meristematic zone at the base of the fruit. This zone is torn in two horizontally, the elasticity of the stretched pericarp comes into play, the 'seed' (its shape helping) is forcibly ejected enveloped by the endocarp. The viscid cells are torn across at their peripheral ends, which are left on the inner surface of the mesocarp. The cell-sap of these cells escapes and gives to the viscid walls a more sticky consistency, by which the seed is enabled to adhere to the host-branch on which it may fall. It has been noticed that the viscid layer is not present at the antiradicular end of the seed.

5. The Male Flower of A. Oxycedri.

Sir W. J. Hooker¹ first figured the male flower magnified ten or twelve times. Examination after greater magnification of a flower just before expansion shows that the stamen consists of a sessile anther, bilocular at first, becoming unilocular by the breaking down of the separating trabecula in the usual way. The wall of the anther consists of one layer of cells only, and it is curious that this, though it is the epidermis,

¹ W. J. Hooker, op. cit. on p. 142, Tab. xcix.

has the fibrous markings typical of the sub-epidermal layer of cells of an ordinary anther (Fig. 13). The tapetum is represented by yellowish brown spheroidal bodies averaging 1/3000 inch in diameter. The structure of the pollengrain at this stage (Fig. 14) comes out very clearly, and is normal. Still further reduction is noticeable of the staminal leaf; the stamen has no vascular bundle. The single vascular bundle of the perianth segment on which the stamen occurs makes a slight bend towards the stamen beneath its insertion, and one or two of the vessels may point a little towards it, but there is no indication of an independent vascular supply in the stamen. On making longitudinal sections of a very young flower, the expansion of which would have happened in the following year, the development of the flower as a whole and of its several parts can be ascertained. The position of the stamen is seen to be very different from that in the expanded flower. It arises as a multicellular lateral outgrowth of the floral axis, independently of the perianth-segment, and acquires its final position by the intercalation of the lower half of the perianth-segment as a belt of tissue common to the stamen and perianth-segment (Fig. 15).

Whilst this observation may do nothing to further the elucidation of the precise nature of the perianth-segment, whether it is a sepal or a petal, it does strongly support Eichler's opinion of the nature of the andræcium in the Visceae:—'The anther of Viscum is so completely fused with the perianth-leaf, even in its early stages, that Hofmeister regards the two as forming only one phyllome. Van Tieghem, who agrees with this determination, quotes in support of it the presence of one vascular bundle in the organ. I must however adhere to the old statement, that we have to do here with a very intimate fusion of two different leaves; for not only in different species of Viscum itself, but also in closely allied genera, Eremolepis, Phoradendron, &c., the two leaves can be so fully isolated that they often show only a faint fusion

¹ Eichler, Blüthendiagramme, p. 556.

at the base, and in these cases the anther returns to the usual form of this organ. Also, it sometimes (exceptionally) happens in those genera that there are flowers with three perianthleaves and only two stamen-leaves, in which case one of the latter is placed in the space between two perianth-leaves; certainly the best evidence against Hofmeister's determination. The superposition of stamens and perianth-leaves can be explained as in Loranthus 1.' In Arcenthobium the stamen is distinct from the perianth-leaf at first, just as it is practically throughout life in Eremolepis. The absence of a vascular bundle in the stamen finds its counterpart in the evascular character of the carpels, which, except for this absence of bundles, have all the characteristics of the carpels of a normal Angiosperm. It is only by a great strain of comparison that the stamens and carpels can be regarded respectively as ligules of the perianth-leaves, or as similar to the integument of the ovule in Coniferae-hypotheses which have been advanced as favouring an affinity of Loranthaceae with Gymnosperms. The comparison of the young and old male flowers of Arceuthobium furnishes one more illustration of the representation of phylogeny in ontogeny: Arceuthobium, one of the most highly modified of the Visceae, passes through a stage in the development of its male flower which is permanently represented in less modified members of the group 2 (e.g. Eremolepis). Allowing for the decrease in the number of layers composing the wall of the pollen-sac, the course of development is normal³ (Fig. 16). There was however an interval of twelve months between the young and old male flowers examined. There were no flowers showing stages intermediate between the archesporial cells and the nearly ripe pollen-grains.

6. VEGETATIVE ORGANS.

The detailed and fully illustrated description of the vegeta-

¹ Eichler, Blüthendiagramme, p. 554.

² Bentham and Hooker, op. cit. on page 138, p. 206.

³ Goebel, Outlines of Classif. and Sp. Morphol., p. 362.

tive organs by Solms-Laubach 1 is exhaustive. The course and structure of the vascular bundles are described and figured by Chatin². Objection to the course of the bundles described by Chatin is taken by Solms-Laubach, who points out that this observer has overlooked the two small lateral vascular bundles in the scaly vegetative leaves. The extremly complicated system of intra-cortical mycelioid branching haustoria is shown by Solms-Laubach to be deducible from the single primary haustorium of the Santalaceae, just as is the case in the other less modified Loranthaceae examined by him. The modification wrought by parasitism in Arceuthobium has not proceeded pari passu in the vegetative and sexual organs. Its intra-matrical vegetative organs present an extreme of modification, whilst its gynæceum is much less affected than that of most other Loranthaceae. I could not find any purely vegetative specimens in the crowded adventitious extra-cortical shoots. The connection between the xylemelements of the parasite and those of the host is easily observed. The radial wall of the xylem-tracheide of the host is split along the middle lamella, so that the fine secondary haustorium with its thin wall has only half the thickness of the tracheide-wall on each side intervening between it and the cavity of the tracheide.

The germination of *Arceuthobium* is unknown. I found one or two ejected seeds on pieces of the host-branch, and in one the radicle showed a distinct curve towards the host-branch, so that *Arceuthobium* is probably in its hypocotyledonary stem negatively heliotropic, and in its root independent of geotropism like *Viscum album*.

Of the thirteen species mentioned by Eichler³ only five or six are regarded as good in the Genera Plantarum of Bentham and Hooker, and of these A. Oxycedri is the most widely

¹ Solms-Laubach, Ueb. d. Bau u. d. Entwick. d. Ernährungsorgane parasit. Phanerog, in Pringsheim's Jahrbücher, vi. 1867, p. 615.

Solms-Laubach, Das Haustorium d. Loranthaceae, etc., in Abh. d. Naturf. Gesell. zu Halle, xiii. 1875, p. 256.

² Chatin, Anat. Comp. d. Végétaux, Paris, 1856-1862, p. 484, Pl. lxvii.

³ Eichler, Fl. Brasil. V, Pars 2, p. 105.

distributed. The general result of the investigation tends to show that in the possibility of the formation of two embryos and in habit the affinity of *Arceuthobium* to *Viscum album* is closer than was generally supposed ¹.

7. SUMMARY.

There is found in the ovary at the time of pollination a basally attached freely projecting conical ovarian papilla, containing two apico-lateral imbedded embryo-sacs in which the contents are arranged as in a normal angiosperm. embryo-sacs arise in each case from a single hypodermal archesporial cell. The morphological value of the contents of the ovary is the same as in Loranthus sphaerocarpus as described by Treub, the papilla consisting of the modified apex of the floral axis and constituting a placenta bearing two buried ovules reduced to embryo-sacs. At no time does the papilla fuse with the wall of the ovary, its apical region becomes a pseud-calyptra to the solitary embryo which is straight, and has an exserted radicle without a root-cap. The dehiscence of the fruit is due in the end to the rupture of a basal horizontal meristematic zone. The seed is covered by the endocarp, the most external layer of which consists of viscid cells, which are severed at their peripheral (distal) ends at ejection of the seed. The sessile anthers in the expanding male flower, with a fibrous epidermis and no vascular bundle, are in the young flower seen to be distinct stamens. carpels like the stamens are evascular, and are opposite, not at right angles, to the perianth-segments. The only points to be added to the complete description of the vegetative organs by Solms-Laubach are the absence (in my material) of any adventitious purely vegetative shoots, the presence of a constant connection of the xylem-vessels of the parasite with the tracheides of the host, and the cleavage of the radial wall of the tracheide of the host by the finest parasitehaustoria.

¹ Jost's paper, Zur Kenntniss der Blüthenentwicklung der Mistel, in Botanische Zeitung, 1888, No. 24, has appeared since this paper was in the press.

EXPLANATION OF FIGURES IN PLATE X. A.

Illustrating Mr. Johnson's paper on Arceuthobium Oxycedri.

Fig. 1. Longitudinal section of pollinated female flower, through the median plane of the perianth-segments. p. s. perianth-segment with vascular bundle. s. c. style and stylar canal, formed by the two carpels. o.p. ovarian papilla. e. s. embryo-sacs. \times 120.

Fig. 2. Ovarian papilla of Fig. 1. e. s. embryo-sac, a vacuole in each. o. oosphere. p. t. pollen-tube, penetrating into apex of papilla. ep. p. epidermis of papilla. Only the egg-apparatus in e. s. is fully figured. × 1020.

Fig. 3. Embryo-sac, a little younger than in Fig. 2, and from a section of the flower made at right angles to the median plane of the perianth segments. o. oosphere. a. c. antipodal cells. × 1020.

Fig. 4. Longitudinal section of the 'ovule.' p. t. primary tapetum cell divided e. s. uninucleate embryo-sac. s. c. two sister-cells of embryo-sac. × 480.

Fig. 5. Longitudinal section of ovarian papilla showing embryo-sac in same stage as Fig. 4. o. p. ovarian papilla. e. s. embryo-sac. i. w. o. inner surface of wall of ovary between which and the papilla is the cavity. \times 480.

Fig. 6. Transverse section of a female flower through the ovarian papilla. $c.\ s.$ the two embryo-sacs opposite the 'fused' perianth-segments. $v.\ b.$ vascular bundle of $p.\ s.$ the perianth-segment. $o.\ p.$ ovarian papilla. \times 120.

Fig. 7. Transverse section of female flower through the style to show the two carpels opposite the two perianth-lobes. c. the carpel. s. c. the stylar canal. p. s. perianth-segment. \times 120.

Fig. 8. Ripe fruit in surface view. a. the zone of dehiscence. b. the line of separation between the sclerotic cells of the mesocarp (a cdot b) and the ordinary parenchyma of the pericarp. The dotted lines indicate the stalk of the fruit enclosed in a pair of scaly leaves. \times 12.

Fig. 9. The same fruit in section. endm. endosperm. emb. embryo. v. s. viscid cells of endocarp. m. c. crushed cells of mesocarp. × 14.

Fig. 10. Longitudinal section of an ejected seed. *endp.* inner part of endocarp. a. o. p. apical part of ovarian papilla, b. o. p. basal part of ovarian papilla. v. c. viscid cells now open at outer ends. *emb.* embryo. *endm.* endosperm. × 120.

Fig. 11. A little of the basal part of the pericarp dotted line at α in Fig. 9. s. m. c. sclerotic cells of mesocarp. α . the meristematic zone at the base of the fruit. endm. endosperm. \times 480.

Fig. 12. Apical part of viscid cells in longitudinal section, showing connection with the crushed mesocarp-cells, m.c. p.v.c. dilated peripheral end of viscid cell. m'.c'. uncrushed mesocarp-cells. l.c. line of cleavage of viscid cells at ejection of seed. \times 1020.

Fig. 13. Longitudinal section through two stamens of male flower just before expansion. $\not p$. s. perianth-segment. st. stamen. v. b. vascular bundle.

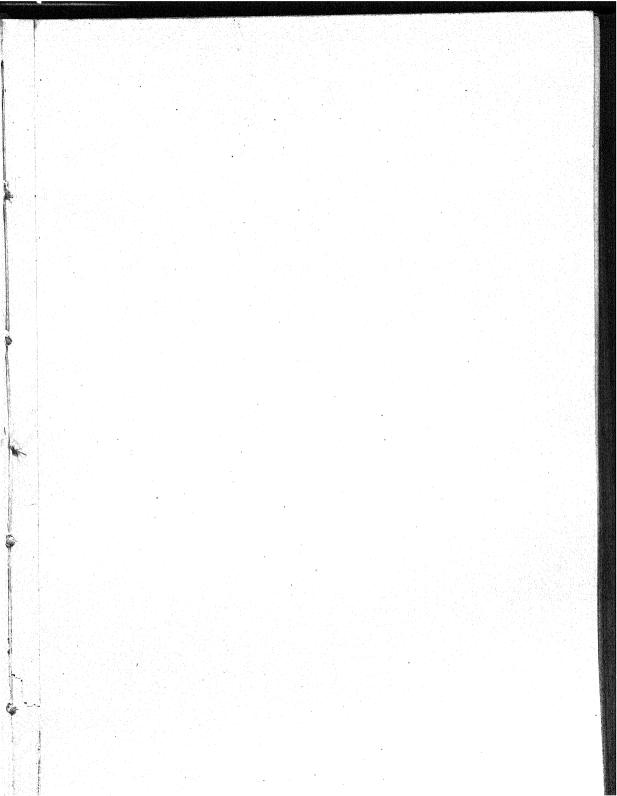
160 Johnson.—On Arceuthobium Oxycedri.

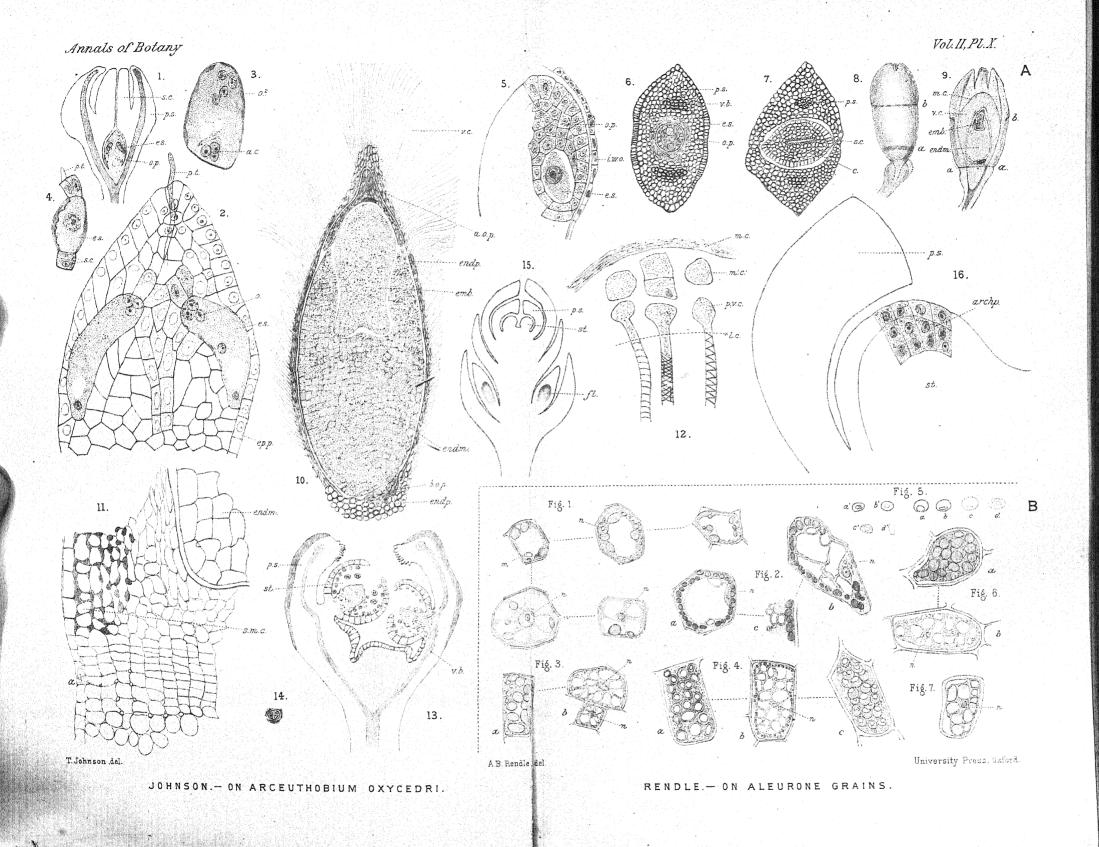
Fig. 13, cont. In the evascular stamens, the fibrous wall, the remains of the tapetum, and a few pollen-grains are shown. \times 120.

Fig. 14. A nearly ripe pollen-grain. Exine, intine, large spheroidal vegetative nucleus and fusiform generative nucleus were all very distinct. \times 480.

Fig. 15. Longitudinal section of a very young male flower. p. s. perianth-segment. st. stamen distinct from perianth-segment, ft. still younger male flowers. \times 50.

Fig. 16. A part of the same more highly magnified. p. s., st. as in Fig 15. archp. archesporium-cells dividing into tapetum and mother-cells of spores. × 1020.







On the development of the Aleurone grains in the Lupin.

ВY

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With Plate X. B.

THE formation of aleurone-grains, the characteristic proteid reserve-material found in seeds, was studied by Pfeffer 1 sixteen years ago. According to his results, the mineral contents, crystals of calcium oxalate, or the 'globoids' of double phosphate of lime and magnesia, first make their appearance in the cell-sap, and then, singly or in groups, act as centres of attraction for the proteid matter, which, as the seed in ripening loses water, is precipitated from the turbid cell-sap. Where proteid crystalloids occur, they too appear in the cell-sap simultaneously with the inorganic solids.

In describing their development in Lupin (referring more especially to L. polyphyllus), Pfeffer says, 'The protoplasmic strands having been converted into ground-substance, the resulting arrangement might at first sight easily suggest the idea that the protoplasm becomes a parenchymatous network whose meshes form moulds for the immigrating metaplasmic substance. But the history of development is opposed to such a conclusion.'

It would appear, however, at any rate in *Lupinus digitatus* which has been investigated in the present instance, that this

¹ Pringsheim's Jahrb. fur Wissenschaft. Bot. Bd. 8. 1872. [Annals of Botany, Vol. II. No. VI. August 1888.] rejected idea is more nearly correct than the conclusion at which Pfeffer eventually arrives, inasmuch as the grains are evidently actually secreted by and in the protoplasm itself.

Until the cotyledons completely fill the seed-coat, there is no trace of the aleurone-grains; the cells contain a conspicuous nucleus slung in the centre by thick protoplasmic bridles or sometimes lying in the parietal protoplasm. In the latter is the layer of chlorophyll-corpuscles in which small grains of starch appear, which, by gradual increase in size and number, have filled the corpuscles by the time the cotyledons have filled the seed-coat. When this stage is reached the seed begins to swell and its outline can be traced through the pod. If we examine sections of the cotyledons at this stage, the cells are seen to contain small spherical or oval bodies partly or wholly projecting from the granular protoplasm, whether the parietal layer, or that surrounding the nucleus or forming the connecting bridles (Fig. 1). These bodies at first appear as little convex protrusions, but rapidly increase in size till spherical or oval bodies are formed more or less embedded in the protoplasm. They stain deeply, more so than the protoplasm itself, with iodine, haematoxylin, Hofmann's blue, and eosin, and the staining is perfectly homogeneous. Nowhere in the cell is there any suspicion of solid mineral matter; crystals of calcium oxalate and globoids are alike absent.

If a section be mounted in iodine and watched while dilute potash (I per cent. or 5 per cent. solutions were used) is run under the cover-slip, the bodies are seen to swell up considerably, and project into the vacuole, while the substance contained in them evidently dissolves. In the now very transparent section their fine clear distended outlines are seen to be in continuity with the protoplasm. If we now carefully wash, by drawing a little water through, and then run in iodine, the section shrinks and again becomes stained, but the deeply staining bodies have gone; we can still see however, especially in the uncompressed cells towards the outside, the delicate stained protoplasmic membranes in perfect

continuity with the rest of the protoplasm and enclosing the cavities from which the soluble matter has been abstracted (Fig. 2). It is therefore evident that the above-mentioned bodies consist of some substance, presumably proteid, soluble in dilute potash, which has been secreted by and in the protoplasm.

If sections be similarly treated with 10 per cent. or saturated solutions of common salt or potassium phosphate, the bodies merely swell up somewhat but are not dissolved, and, if washed in water, even after lying for twenty hours in the salt solutions, appear quite unaltered. I per cent. and 10 per cent. solutions of hydrochloric acid, even after twenty hours' action, only cause slight swelling. The bodies therefore differ in solubility from the grains of the ripe seed, which are completely and at once soluble in such solutions.

After solution a perfectly clear space is seen to remain, and there is no sign whatever of crystalline or globoid contents.

These bodies, which, as the sequel shows, are the primitive aleurone-grains, increase in size and number and soon fill up the vacuole, so that the cell contains within the parietal layer of protoplasm a number of roundish grains quite separated from each other by a protoplasmic reticulum, made up of the bridles and the membranes originally separating the secretion from the vacuole. By watching a section in which this stage has not quite been reached, while dilute potash is run under the slip, the limiting protoplasmic membranes of adjacent or opposite masses of the secretion are seen to swell out and meet to form what has now every appearance of a protoplasmic strand, indicating how the same would take place in the ordinary process of growth. Near the centre, or sometimes at the side, is seen the nucleus, which is becoming more or less compressed by the growing grains; these relations are clearly brought out by iodine, and the protoplasmic network demonstrated by running in dilute potash which at once dissolves the grains, leaving quite empty cavities.

By the time the vacuole has been nearly filled up, a dif-

ference in solubility is noticed, the grains now reacting like those of ripe seeds, dissolving completely in 10 per cent. and saturated solutions of common salt and potassium phosphate, and also in I per cent. of hydrochloric acid, though still insoluble in water. One gets sometimes preparations in an intermediate state with the grains only partly soluble, even after twenty hours' exposure to the reagent. It has been shown 1 that the aleurone-grains of ripe seeds contain several distinct proteids belonging to the albumose and globulin groups, and the change in solubility during development may be the expression of the breaking down of some complex proteid substance, originally secreted by the protoplasm, into the several simpler proteids known to occur in the ripe seed, and it is during this process that one would expect the separation of solid mineral constituents to take place in cases where they are found in the ripe seed. The grains continue to increase in size but are at first rather watery, and in absolute alcohol material show a vacuolation, probably due to the reagent, the denser part forming an external ring, or very often collecting chiefly on one side and forming a crescent (Fig. 4); the ring or crescent stains well with the above-mentioned dyes, while the portion inside remains clear. On solution, however, the denser portion is seen gradually to diffuse throughout the whole, forming a homogeneous structure (Fig. 5); when this stage is reached the seed is beginning to get ripe, as indicated by the end of the radicle turning yellow. As ripening goes on the denser part encroaches more and more on the clearer, and by the time the yellow coloration has extended up the radicle and is affecting the cotyledons, the majority of the grains have again come to stain homogeneously, as in the ripe seed, indicating increase in quantity of the denser part and loss of water of the grain coincident with the general drying of the seed. The protoplasm has meanwhile been diminishing, and the starch-grains have by the end of this process disappeared, drops of oil

¹ Vines, Journal of Physiology, III, 1881.

having however been formed. In the ripe seed the grains, which are roundish or somewhat angular through mutual compression, are still separated by a protoplasmic network in which oil-drops occur, while starch is wanting. Hanstein's solution brings out the network and nucleus very well, staining these a deep violet, while the grains scarcely stain at all (Fig. 7).

Solid inorganic constituents were repeatedly sought for, but without success. Sections of the ripe seed, from which the oil had been removed by ether, were treated on a slide with I per cent. of potash, which was allowed to diffuse in so as not to wash away any small globoids which might be present; individual cells or grains were carefully watched meanwhile, sometimes under Zeiss' F objective, at others under the D, but in all cases an empty space was left in the protoplasmic network after solution. Some granules scattered over the section, but especially, and almost exclusively, near the few cell-layers with very granular contents beneath the epidermis, and with no definite relation to the grains, proved to be small starch-grains washed out from these cells. No crystals could be detected by double refraction when such a section was examined under a polarising microscope. Hence we may conclude that the aleurone-grains of Lupinus digitatus have no solid mineral contents. From the foregoing facts it appears that the presence of mineral matter is of very secondary importance in the development of the grains, whereas in the process as described by Pfeffer the mineral matter was essential, forming the point of attraction for the aggregation of the proteid. But Pfeffer's suggestion is too mechanical, and moreover gives no reason whatever for the fact that the grains in the ripe seed are always embedded in a protoplasmic matrix; they should rather be lying loose in the vacuole.

The earliest stage, namely, secretion in the protoplasm of matter soluble only in dilute potash, has also been observed to occur in precisely the same way as above described in another species of lupin (? L. varius).

It is most interesting to note that the development of

aleurone-grains described here corresponds most closely with the manner of secretion of mucilage as lately described ¹ by Gardiner and Ito in the glandular hairs of *Blechnum* and *Osmunda*; in both cases the secretion is strictly intraprotoplasmic, both the aleurone-grains and mucilage-drops moreover remaining, after secretion, quite separate in a reticulum of protoplasm. In both cases too there is some chemical change in the originally secreted substance, before the final product is formed.

The seeds used in these investigations were preserved in absolute alcohol; 2 per cent. chromic acid material shows the early stages very well, but as the grains begin to increase in size, the cells are seen to be full of empty rings, an appearance which is maintained up to the time when the seed is fully ripe; the grains are moreover rendered quite insoluble, even in the ripe seed, in salt solutions and 5 per cent. potash. By placing sections of the ripe seeds, preserved in alcohol, in 2 per cent. of chromic acid solution, the homogeneous grains are converted into rings, which now resist for several minutes the action of 5 per cent. potash and remain undissolved, even after twenty hours, in saturated salt solution.

The development of aleurone-grains in general is obviously not completely indicated above, as no account is taken of the time and manner of appearance of the globoid and crystalloid, which may both be present, as e.g. in *Ricinus communis*, though *Lupinus digitatus* has neither. I hope to work out these points also, in the summer, when material can be procured.

To judge from the title², which alone I have seen, and that only a few days since, my results agree with those arrived at in a paper by Wakker.

¹ Annals of Botany, I. 1. 1887.

² Aleuronkorrels zijn vacuolen,' in Maandblad voor Natuurwetenschappen, Nos. 5 and 6, 1887.

EXPLANATION OF FIGURES IN PLATE X. B.

Illustrating Mr. Rendle's paper on the development of Aleurone-grains in the Lupin.

Fig. 1. First stage in formation of aleurone-grains in *Lupinus digitatus*. Drawn from a preparation stained with Hofmann's blue. Portion *m*, unshaded, not in focus. The bodies mentioned in the text are line-shaded. Zeiss' D objective and ocular 4. *n*, the nucleus.

Fig. 2. Same stage as the last, showing the little pockets in the protoplasm from which the secretion has been dissolved out by dilute KOH. Now in iodine. The swollen starch-grains shaded dark. a and b same magnification as in Fig. 1. c under F objective. n, the nucleus.

Fig. 3. A little older than the above, grains filling up the vacuole. a and b both from preparations stained with Hofmann's blue; b, after action of dilute KOH showing the protoplasmic network. D objective, ocular 4. Colourless starchgrains seen in the protoplasm lining the wall.

Fig. 4. The growing grains largely fill the cell. In it are seen the grains vacuolated as described in the text, and colourless starch-grains in protoplasm, after staining with Hofmann's blue. b, after solution of grains with dilute KOH, and staining of protoplasmic network with iodine. Swollen starch-grains lining the wall. n, the nucleus. D objective, ocular 4. c a little older than it.

Fig. 5. Shows progress of solution of two vacuolated grains, in dilute KOH on the left, in 10 per cent. of salt solution on the right. D objective, ocular 4.

Fig. 6. From a nearly ripe seed. α , a cell before, b, one after action of dilute KOH. α shows the deeply and homogeneously stained grains, b the protoplasmic matrix and nucleus, n. The colourless drops are oil. D objective, ocular 4.

Fig. 7. From a quite ripe seed stained with Hanstein's solution. Nucleus and protoplasmic matrix have stained a deep violet, the wall a lighter colour, the grains almost perfectly colourless. n, nucleus. D objective, ocular 2.



On the structure of Spongocladia, Aresch. (Spongodendron, Zanard.), with an account of new forms.

BV

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ANI

LEONARD A. BOODLE, A.N.S.S.

(With Woodcuts 8, 9, 10, and 11.)

TNDER the name of Spongodendron, Zanardini¹ established in 1878 a genus of Siphoneae from specimens collected by Dr. Beccari in New Guinea. In the course of the work of one of us at the above group, it became necessary to see specimens or drawings of this type which should give more information than the short description in the Nuovo Giornale. On applying to Dr. Beccari, he at once with the greatest kindness and courtesy sent specimens of the two species S. crassum and S. dichotomum described by Zanardini. On examination they proved to belong to the remarkable genus Spongocladia of Areschoug, described by him in 18532. Only one species of this genus, S. vaucheriaeformis, has been recorded hitherto, and specimens of it collected at Mauritius (whence Areschoug's material came) by Col. Pike are in the herbaria of the British Museum and Kew. Spongocladia can hardly be said to be siphoneous, and so it follows that

[Annals of Botany, Vol. II. No. VI. August 1888.]

¹ Phyceae Papuanae novae, etc., in Nuovo Giorn. Bot. Ital. x.

² Oversigt af Kongl. Vetensk. Akad. Förhandl. Stockholm.

Zanardini's genus is not only merged in Areschoug's, but the type disappears from the group of Siphoneae. At first sight, however, it looks so like certain members of the group that there is ample room for mistake. It may be recalled indeed in justification of Zanardini's opinion that in 1886 one of the present writers found with the Kew specimens of S. vaucheriaeformis a note by the late Professor Dickie, proposing to found on them a new species of Rhipilia—though

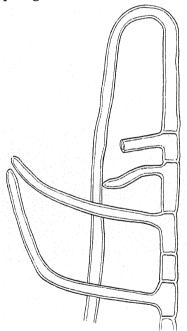


Fig. 8. Filament of Spongocladia vaucheriaeformis, Aresch.

subsequent examination, as shown by his own herbarium in the British Museum, enabled him to correctly place the form under Areschoug's name, which it bears in his published list of Algae of Mauritius 1. This likeness will be understood from the following description.

The thallus of *S. vau-cheriaeformis* consists, as Areschoug pointed out, of long, filiform tubes so interwoven as to form a number of irregularly dichotomous branches, the whole recalling in appearance a digitate sponge. These branches are of the thickness of well-grown specimens of *Codium*

tomentosum, though another species about to be described resembles this Alga much more strikingly. The tubes of which the branches are composed are septate below, and short lateral branches are given off at about right angles from the cells, often on the same side of the filament from three or four

¹ Linn. Soc. Journ. Bot. xiv.

successive cells, their insertion being sometimes at the upper end, as in Cladophora, or the middle. At times, however, the diameter of a branch is nearly as great as the length of the cell from which it takes its origin. The lateral branches, which are sometimes again branched irregularly, probably serve to bind more closely together the interwoven filaments. This function is more effectually performed by certain other branches which become permanently attached to the surface of adjacent tubes by numerous, short, rhizoid processes. This possibly explains the anastomosing described by Zanardini. Above the septate portion of the filament

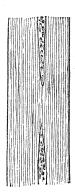


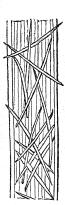


Fig. 9. Portion of filament of Spongo- Fig. 10. Zoospores of Spongocladia cladia vaucheriaeformis, showing obliteration of lumen.

vaucheriae form is germinating in situ (after Areschoug).

there is commonly found one cell longer than the others, and above that again the main portion of the tube-the terminal cell—of great length without cross-partition of any kind, and very closely resembling in this respect as well as in its comparatively great diameter, and the nature of its contents. the tubes of a Vaucheria. Throughout the course of the tube it is much wrinkled lengthwise. Some of the wrinkling is probably due to drying, but there are also finer markings which seem to represent fibrillar thickening of the cell-wall. This structure is seen when a filament has been broken by stretching, and fine threads are left projecting from the broken edge. Areschoug's figure 5 shows the cell-wall resolved into fibrillae by the action of sulphuric acid. The cell-wall in the older parts of the filaments is very much thickened, and in optical section shows numerous layers of stratification without the use of a reagent. This thickening frequently goes so far as to nearly obliterate the lumen, and sometimes this actually happens (Fig. 8).

Areschoug figures what he regards as zoospores germinating in situ in a terminal cell. We have observed an appearance which must be a later stage of the process. Here two intercalary cells, which are about twice their diameter in length, are filled with a densely packed mass of tubular cells with delicate walls, containing chlorophyll. Owing to the crowding of the mass it could not be distinctly resolved, but it appeared



to consist of rather elongated and interwoven tubes. Possibly a small colony of tubes is formed by the division of the contents into zoospores, which germinate inside the mothercell, and increase in size until they burst it. Zanardini mentions terminal and other coniocysts. We are not quite sure what he does mean, but on lateral branches globular terminal cells occur here and there which may possibly have a reproductive function.

The appearance however which we venture to think possesses special interest is presented by the groups of siliceous spicules Spongocladia vauche-which plentifully strew the course of the riaeformis with sponge spicules (after Areschoug.)

The appearance however which we venture to think possesses special interest is presented by the groups of siliceous spicules. These were noted by Areschoug, and also the further fact that the grey

choug.) and also the further fact that the grey compact appearance of the apical portions of the branches is owing to the dense occurrence of these (obviously) sponge-spicules—which moreover cause the whole thallus to feel hard to the touch—like a fresh sponge in short. Areschoug does not appear to have satisfied himself as to the origin of these spicules beyond supposing that they belong to a sponge. They are manifestly far more abundant than is consistent with a merely accidental presence. Mr. Kirkpatrick

of the department of Zoology, British Museum, kindly undertook to compare them with the spicules of other sponges, with the result that he found them to agree most closely with the spicules of a Halichondrine sponge. Not only this, but traces were soon discovered in abundance of the presence of the sponge itself, especially investing the whole of the apical portions of the branches of the thallus, giving them that characteristic grey and compact appearance already noted. Each branch bears therefore, without exception, a cap of sponge bristling with spicules, and from the presence of these throughout the whole body of the Alga it may be inferred that with the growth of the branch the cap is carried upward, while groups of spicules and portions of sponge remain attached to the sides of the tubes. Of course, it is not to be forgotten that sponges frequently are to be found on Algae, and Mr. Kirkpatrick showed us, as being much to the point, Halichrondria panicea growing on Fania, as it may be seen on our own shores. In Spongocladia, however, there is an intimate relation of sponge with Alga of such a character as to suggest at least further inquiry. Accordingly the specimens of Spongodendron were brought into evidence. They came from another part of the world—from New Guinea. These, as has been said, are of two kinds, S. crassum, Zanard., which we find indistinguishable from Spongocladia vaucheriaeformis, by which name it will now be known, and S. dichotomum, Zanard. which now becomes Spongocladia dichotoma, Nob.

In this New-Guinea specimen of S. vaucheriaeformis (Spongo-dendron crassum, Zanard.) we have been unable to find in the limited portion at our disposal any trace either of an apical cap of sponge or indeed of sponge-tissue. But here again sponge-spicules are abundant, though not so much so as in the Mauritius specimens. The spicules are those of another sponge. In S. dichotoma from the same locality spicules also are present to much the same extent, and they are those of yet another sponge. (It may be mentioned here that in S. dichotoma the walls are thinner and the septation

and branching of the filaments less frequent.) In addition to these forms Dr. Grunow very kindly sent us another species, not hitherto published, which he had collected in New Caledonia, which we have described under his name of S. neocaledonica. Its habit is more diffuse, and in fact the thallus can hardly be described as branching at all. The filaments which compose it are of great diameter and contain abundance of starch. In this form we find still fewer spicules and no trace of sponge. The spicules here again belong to a sponge different from all the others.

Are we to regard this occurrence of sponge and of sponge-spicules in all these instances as accidental? Taken by itself, the case of S. neocaledonica, for example, we confess might easily be so explained. Taken together with these other forms from other parts of the world in which spicules were more abundant than they usually are on Algae growing among sponges; taken especially with the case of S. vaucheriaeformis, we venture to think the subject presents another aspect. It is possible that we have here some biological relation between sponge and Alga. Farther than this suggestion of inquiry we should not be justified in going on the material at our command. It would certainly be interesting to know whether such biological relation, if any, is concerned with nutritive adaptation.

We append a systematic account of the genus, in which we have adopted so far as possible the descriptions of Areschoug and Zanardini. Areschoug's generic characters have been so amended as to admit S. neocaledonica. As to its systematic position it is scarcely advisable to speak very definitely, but it certainly appears to come nearer Cladophora than any other type known to us.

Spongocladia.—Aresch. in Oversigt af Kongl. Vetensk. Akad. Förhandl. 1853.

Alga viridis, adnata, filis cellularibus laxe implexis contexta. Fila unica cellularum serie constructa, inferne parce

ramosa, acrogenia; cellulae inferiores breviores, superiores longissimae, tubuliformes, vaucheriaeformes, utraeque intus granulis chlorophyllinis vestitae. Schizogonidia seu zoosporae in cellulis tubuliformibus formatae.

Syn. Spongodendron, Zanard. Nuovo Giorn. Bot. Ital. x. p. 37.

1. S. VAUCHERIAEFORMIS, Aresch. loc. cit.

Thallus extus coloris griseo-flavescentis l. griseo-albidi, intus viridis, 3–4 pollicaris, caespitosus, a basi digitato-dichotomus, 2–4 lineas crassus, teres l. compressus, apicibus nunc subattenuatis, nunc incrassatis l. incrassato-truncatis.

Syn. Spongodendron crassum, Zanard. loc. cit.

Hab. ad litora insulae Mauritii, Lithothamniis innascens (Areschoug; Pike!) et ad Sorong (non ins. Aru) Nova Guinea (Beccari!).

2. S. DICHOTOMA, Nob.

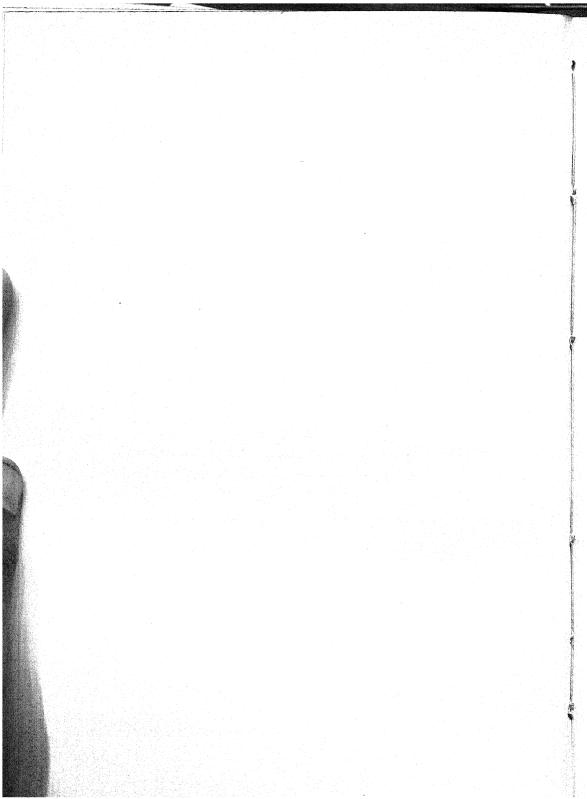
Thallus gracilis, filiformis, irregulariter dichotomus, segmentis elongatis distantibus ad axillas parum dilatatis, huc illuc invicem conglutinatis, apice valde attenuatis, filis frondem constituentibus tenuioribus conspicue articulatis. Facies omnino *Codii tomentosi*.

Syn. Spongodendron dichotomum, Zanard. loc. cit. Hab. ad Soroñg, Nova Guinea (non ins. Aru) (Beccari!).

3. S. NEOCALEDONICA, Grun. in litt.

Thallus compactus, vix ramosus, extus coloris griseo-flavescentis, intus viridis, 2-3 pollicaris; filis frondem constituentibus crassis, haud in ramos distinctos implicatis.

Hab. ad Poro, Nova Caledonia (Grunow!). Prope litus, aqua non semper obtecta, crescens.



Notes on the Geological History of the Recent Flora of Britain.

вv

CLEMENT REID.

H AVING had occasion some years since to study the plants of our latest Pliocene deposit—the Cromer Forest-bed—and more recently the flora of several deposits between that ancient period and the present time—I thought it would be of interest to collect any information that might throw light on the questions: What plants are truly native? What are the variations of climate that the plants show? What can we learn as to differences of geographical distribution of the living species in past times?

Of course these questions will take many years of work to answer, but the material already collected seems of sufficient importance to justify the publication of the following notes.

Instead, therefore, of attempting at present to analyse the flora of the different beds or periods, as originally intended, these notes have been put together in the form of a record of anything that is known of the geological history of each species.

A good many plants have been incidentally recorded from old alluvial deposits in archæological or geological papers, but I have commonly found that the specimens were lost, or were never preserved, or still more often were never properly determined. It has therefore been necessary to confine these notes to specimens that I have examined, and which may still be found in some collection, so that any mistakes can be rectified. The only exceptions are in favour of a few species recorded by competent botanists.

With regard to the beds from which the plants were [Annals of Botany, Vol. II. No. VI. August 1888.]

obtained, only those are included that date from a period previous to the Roman occupation. This limit was fixed on the ground that the Roman invasion and the constant going to and fro which followed it, must have greatly assisted the spread of weeds of cultivation. Of course many weeds of cultivation must have come in at an earlier period, when cereals were first introduced, but nearly all the deposits from which plants have been examined, seem to be of a much more ancient date. The newest 'submerged forest' is probably the most modern deposit from which material has been obtained, and this submergence dates fully 3000 years since.

To the officers of the botanical department of the British Museum, especially to Mr. Carruthers and Mr. Ridley, I am indebted for much assistance in the determination of many of the more obscure fossils. The specimens being usually only seeds, or the hard parts of the fruit, often strangely altered in decay, this has been a very difficult task. The specific determination is comparatively easy, but it is sometimes very difficult to obtain a first clue in the form of an ordinal or generic character, very similar seeds sometimes occurring in several different orders—e.g. Caryophylleae and Chenopodiaceae. Mr. Carruthers has kindly undertaken the determination of the Grasses, so the species of that order are given on his authority.

Specimens have been received from so many sources, that it is impossible here to mention all of them. The most important contributions were those from Mr. Jas. Bennie, of the Geological Survey of Scotland, who has most industriously collected the seeds and other fossils from a number of Scotch Pleistocene deposits. These specimens are all preserved in the collection of the Geological Survey in Edinburgh 1.

From other Scotch localities I have received specimens from Messrs. David Robertson, J. C. Howden, Robert Craig, and Thomas Scott, and also from the Hunterian Museum at Glasgow.

¹ By permission of the Director-General I have been enabled to make use of the material in the preparation of these notes.

The specimens from Southampton Dock were received from Mr. Whitaker; those from the Tilbury and Albert Docks from Mr. Spurrell. Those from other English localities are nearly all of my own collecting.

AGE OF THE PLANT-BEARING DEPOSITS.

Roughly, the deposits from which plants have been obtained may be divided into Postglacial, Interglacial, and Preglacial.

The first group includes the 'submerged forests,' and contemporaneous upland deposits; raised marine deposits, like the Clyde beds; and beds with arctic plants, lying directly above the latest boulder clay of the district. This group is apparently separated from the next one by a period of intense cold.

The second group includes all beds which underlie boulder clay, but are newer than the Cromer Forest-bed. These are cut off from both the newer and older deposits by periods of intense cold and glaciation. With these may be classed the bed with arctic plants which underlies the lowest boulder-clay in Norfolk.

The third group contains the Cromer Forest-bed, which underlies all the glacial deposits, and forms the highest portion of the Pliocene formation.

It is not suggested that the different beds in each group are exactly contemporaneous, but that they occupy somewhat similar positions in the series. For instance, further study may show that there are several interglacial periods grouped together in section 2, but at present I see no means of separating them. Some of the postglacial deposits in the south of England may also be equivalent to interglacial deposits further north. But this point also cannot yet be settled.

Commencing with the newest group, the prehistoric peat of the mountain districts has been very imperfectly searched, the only sample examined being one given me by my colleague, Mr. George Barrow. This was obtained thirteen feet down in the peat at Corb, in the Highlands, at a height of over 1400 feet above the sea. It yielded a few upland plants, but only species still found in similar situations.

At the base of similar hill-peats in the Yorkshire moors, large well-grown oaks are found, but the associated seeds have not been collected, and it is doubtful whether the oaks alone are sufficient evidence of a change of climate.

From the raised marine deposits with arctic shells bordering the Firth of Clyde, I have determined fifteen species, principally sent me by Mr. Thomas Scott and Mr. Bennie. Though associated with a decidedly northern marine fauna, there is nothing arctic about the plants. At that time the temperature of the air was apparently higher than that of the sea in the Clyde district. The plants, though few, are interesting, for they include dry-land forms—such as Bartsia Odontites and Thymus Serpyllum—not known from any other localities.

The 'submerged forests' and associated deposits in Holderness yield a few species, all still living in the district. But from another bed in the same part of Yorkshire, *Betula nana* has been obtained, at Bridlington by Dr. A. G. Nathorst, and at Holmpton by myself.

In Norfolk a few plants occur in a postglacial river-deposit at Mundesley, associated with the elephant and river-tortoise; and Mr. H. N. Ridley and I have lately obtained a number of others from Hoxne, but have not yet finished the determination.

From peat below the sea-level at the Albert and Tilbury Docks, I have received a few specimens from Mr. Spurrell. All the species are still living in the neighbourhood.

A sample of similar peat from Southampton Docks, given me by Mr. Whitaker, yielded a few widely distributed species.

The different localities from which interglacial plants have been obtained are nearly all in Scotland. This is largely due to the thorough way in which the Scotch glacial deposits have been searched, for similar beds certainly occur in England, though the plants of the only one I have been able to examine were nearly all too much decayed for determination.

Kilmaurs, in Ayrshire, is probably the most celebrated of these interglacial deposits ¹. Here, beneath a thick bed of till, and associated with a tusk of mammoth, a number of seeds were found. Mr. John Young, of the Hunterian Museum, has given me the opportunity of examining the original specimens, and I have also received some others from Mr. Bennie. The number of species, however, only amounts to six, all plants of wide range.

The most interesting, botanically, of all the Scotch interglacial deposits are found at Redhall and Hailes quarries, about three miles from Edinburgh.

The peaty mud at the first of these localities occurs beneath a mass of boulder clay, the position of which both Dr. Arch. Geikie and Mr. Howell assure me cannot be accounted for by any landslip or similar cause. This question it was very important to settle, for a large number of species occur in the interglacial peat at Redhall, that are elsewhere unrecorded in a fossil state from beds of any age. Two of these species till now have been considered recent introductions into Britain.

Through the industry of Mr. Bennie, we can now form a very good idea of the flora of this period, for he has sent me the fruits and seeds of no less than forty-six species of flowering plants from Redhall, besides ten or fifteen not yet determined. They occur, associated with elytra of beetles and caddis-cases, felted together with Mosses. There are no mollusca or mammals, but probably the peaty water has dissolved all calcareous organisms. It is to be hoped that before long Mr. Bennie may be able to publish a full account of his interesting discoveries in these interglacial deposits.

The whole of the plants from Redhall are still native of the Scotch lowlands, with the exception of *Galeopsis Tetrahit* and *Carum Carui*. However, the recent distribution of these two species makes it surprising, not that they are found fossil in an interglacial deposit in Britain, but rather that they are not

¹ See R. Craig and John Young, in Trans. Geol. Soc., Glasgow, vol. iii. p. 310.

truly natives of Britain now, if such really be the case. Still, it must not be forgotten that the occurrence of a plant in these interglacial beds, does not prove that it ought to be accepted as a native of this country in postglacial times, though it may be good evidence that it was not first brought to this country as a weed of cultivation. Between the interglacial and postglacial periods there occurred a period of glaciation, during which a large portion, probably most, of the native plants were exterminated, to be reintroduced when the climate ameliorated.

The peaty bed from which the plants were obtained in the neighbouring quarry of Hailes, though probably of about the same age, does not now lie under boulder clay. However, in a letter dated September 28th, 1887, Mr. Bennie writes that 'Hailes quarry is very large, and in the south side of it a few years ago there was exposed a peat bed interbedded in boulder clay, as described and figured in "Prehistoric Europe"' [by Prof. James Geikie]. The occurrence of Salix herbacea and abundance of Isočies, neither of which are found in the neighbourhood now, shows that the peat is, at any rate, no modern deposit, and I think it may be classed provisionally with the interglacial beds. It is unfortunate that the bed of peat actually under boulder-clay is not now visible, and cannot be searched for plants.

Mr. Bennie has sent me twenty-five species of flowering plants from Hailes, besides several still undetermined. With the two exceptions already mentioned, they are species still found in the lowlands, though the absence of all, except such as have a considerable northward range, is suggestive of a climate somewhat colder than that of the south of Scotland at the present day. The flora of the extreme north of Scotland is more similar.

A similar peaty bed between two masses of boulder-clay has recently been described by Mr. Robert Dunlop, as occurring at Airdrie, near Greenock ¹. Through the kindness of Mr. Dunlop and Mr. Bennie I have been able to examine the plants, but find the flora is poor, the majority of the specimens

¹ See Trans. Geol. Soc., Glasgow.

belonging to two species, *Hippuris vulgaris* and *Carex rostrata*. The occurrence of *Betula nana* gives a somewhat northern character to this flora.

There is one other deposit which provisionally, and with great hesitation, has been placed in the interglacial division. This is the well-known peaty bed of Cowden Glen, in Renfrewshire, so well described in Mr. Craig's paper 1. At the present day this old lacustrine deposit certainly lies beneath a boulderclay, but the question has arisen—to what extent is this overlying boulder-clay merely the remains of a landslip? The bed is certainly ancient, for it contains remains of the Megaceros and Bos primigenius; but Mr. John Young points to the landslips that still occur as sufficient to account for the overlying boulder-clay. Prof. Jas. Geikie, Mr. Craig, and Mr. Bennie, on the other hand, consider that part, at least, of this overlying boulder-clay is in place. The plants do not throw any light on the question, for they are all species still living in the district.

Mr. Bennie has sent me a large number of specimens from this locality; but Mr. Mahony has recorded several species that I have not seen, and I cannot now learn what has become of them.

Older than any of the deposits already mentioned, there is another bed with Salix polaris and other arctic plants lying at the base of the whole of the glacial deposits of Norfolk, and proving the existence of very arctic conditions previous to the formation of the first till or boulder-clay. This was first discovered at Mundesley, in Norfolk, by Dr. A. G. Nathorst. Afterwards, by following his instructions, I was enabled to add a few other species, including Betula nana, and also to trace the same plants in two fresh localities—at Beeston, three miles west of Cromer, and at Bacton, four miles south of Mundesley 2. At present this bed has not been traced beyond the Norfolk coast.

¹ Trans. Geol. Soc., Glasgow, vol. iv. p. 17. See also J. A. Mahoney, Organic Remains found in Cowden Valley, in Geol. Mag. vol. vi. p. 390.

² See Memoirs of the Geological Survey—Geology of Cromer, p. 83.

Still older, and beneath the whole of the glacial and arctic deposits, we find the preglacial 'Cromer Forest-bed,' with elm, beech, oak, pine, and spruce. This flora has already been described, though I have taken the opportunity to bring the account up to date, and to make a few necessary corrections.

In the flora of the Cromer Forest-bed, we find for the first time a marked admixture of species no longer found in Britain, and also a certain number which there is every reason to believe are now entirely extinct, though, in the absence of generic or ordinal characters, I do not propose to describe them, or give them new names.

This oldest representative of the living flora of Britain is associated with a number of large mammals, most of them extinct, and many characteristic of the Newer Pliocene period. Many of the mollusca are also extinct.

Unfortunately, at this interesting point of our enquiry we are stopped by the imperfection of the geological record, which is so great that not a single recognisable plant has been obtained from any deposit in Britain lying between the Upper Pliocene and the Middle Oligocene². When plants are again met with the flora has a sub-tropical character, and is quite unlike that now found in Britain.

DICOTYLEDONS.

THALICTRUM MINUS, Linn.

Numerous very acute achenes of *Thalictrum* have been formerly referred to this species. They may, however, belong to the sharp-fruited variety of *T. flavum*. Horizon—Cromer Forest-bed. Localities—Sidestrand and Mundesley (C.R.).

THALICTRUM FLAVUM, Linn.

The small blunt achenes of this species are very common in the preglacial beds. Horizon—Cromer Forest-bed. Localities—Sidestrand, Mundesley, Ostend, and Pakefield (C.R.),

¹ Trans. Norfolk Nat. Soc. vol. iv. p. 189.

² The so-called Miocene Floras of Bovey Tracey and Mull, according to Mr. Gardner, are probably of Eocene age.

RANUNCULUS AQUATILIS, Linn.

Very abundant in most lacustrine deposits. Several varieties are found fossil, but the characters of the fruit in the recent forms do not seem to be sufficiently constant to allow of any determination of sub-species from fruit alone. Horizons—Cromer Forest-bed, passim; Scotch interglacial beds, passim.

RANUNCULUS SCELERATUS, Linn.

Two detached carpels from Hoxne in Suffolk, in a lacustrine deposit overlying boulder-clay, were found by Mr. Ridley and myself. Unknown elsewhere fossil.

RANUNCULUS FLAMMULA, Linn.

Mr. Bennie has sent me numerous carpels from Redhall and Hailes quarries, and one badly-preserved specimen from Cowden Glen. Badly-preserved fruits, apparently belonging to this species, also occur in more modern peats. Horizons—postglacial and interglacial (not yet found in preglacial beds).

RANUNCULUS LINGUA, Linn.

A few detached carpels have been found at Redhall, near Edinburgh, in interglacial beds.

RANUNCULUS REPENS, Linn.

Detached achenes. Postglacial beds of Garvel Park, on the Clyde, and Hoxne, in Suffolk. Interglacial beds, Redhall and Hailes, near Edinburgh. Preglacial, in Cromer Forestbed, at nearly all localities.

In shape and sculpture of the achenes, R. repens is so similar to R. bulbosus and R. acris that great care is needed to distinguish between them, especially when the beak is missing. The slight differences seem, however, to be quite constant, and all the specimens belong to R. repens.

CALTHA PALUSTRIS. Linn.

Seeds are not uncommon in the interglacial beds at Redhall.

NUPHAR LUTEUM, Linn.

Seeds are common in a postglacial river deposit at Mundesley, and also in the preglacial Cromer Forest-bed at nearly all localities. I have not seen any from interglacial beds.

[NYMPHAEA ALBA, Linn.]

Recorded by Heer as occurring in the Cromer Forest-bed at Happisburgh. The seeds may have been obtained from a recent alluvial deposit at that locality. No specimens have been found in the larger collections made within recent years, and I do not know of any trace of this species in Britain in deposits older than the recent alluvium.

LYCHNIS DIURNA, Sibth.

One well-preserved seed from Redhall, and two from Hailes, in interglacial beds.

LYCHNIS FLOS-CUCULI, Linn.

Postglacial beds of Garvel Park, on the Clyde, eight seeds received from Mr. Thomas Scott. Interglacial beds of Redhall, three capsules and numerous seeds received from Mr. Bennie.

STELLARIA AQUATICA, Scop.

Three seeds, from the preglacial Cromer Forest-bed at Beeston.

STELLARIA MEDIA? Linn.

A badly-preserved compressed seed, shows concentric lines of tubercles becoming obsolete towards the centre, and forming a double keel on the periphery, as in *S. media*. Interglacial, Hailes, near Edinburgh.

OXALIS ACETOSELLA, Linn.

One seed. Interglacial, Redhall, near Edinburgh.

PRUNUS COMMUNIS, Huds.

A few stones. Preglacial (Cromer Forest-bed), West Runton, Happisburgh, and Pakefield.

PRUNUS PADUS, Linn.

A few stones. Postglacial, Hornsea and Sand le Meer, in East Yorkshire. Interglacial, Hailes, near Edinburgh, and Airdrie.

RUBUS IDAEUS, Linn.

Stones (often split by birds or rodents). Postglacial, Clyde beds at Black Burn, East Tarbet (from Mr. Robertson), and Garvel Park near Greenock (from Mr. Scott). 'Submerged Forest,' Southampton Docks (from Mr. Whitaker). Old lacustrine deposit, Hoxne in Suffolk (C. R. and H. N. Ridley). Interglacial beds, Redhall (abundant) and Hailes (rare), (from Mr. Bennie).

RUBUS FRUTICOSUS, Linn.

One stone at each locality. Interglacial, Hailes, near Edinburgh. Preglacial (Cromer Forest-bed), Pakefield, and Mundesley.

POTENTILLA TORMENTILLA? Neck.

One stone. Postglacial (Clyde beds), Roxburgh Street, Greenock.

POTENTILLA COMARUM, Linn.

Achenes retaining their white colour. Interglacial, Redhall (common), and Airdrie.

POTERIUM OFFICINALE, Hook.

One well-preserved fruit at each locality. Preglacial (Cromer Forest-bed), Mundesley, and Sidestrand.

[CRATAEGUS OXYACANTHA, Linn.]

Recorded by Hugh Miller from postglacial brick-clay of Portobello. I have not been able to examine the specimen (said to be wood), and cannot find any trace of the hawthorn elsewhere. The fruits of the hawthorn are so hard, and are scattered so widely by birds, that it is difficult to understand its absence from prehistoric deposits, or at any rate its great scarcity, if the tree is really native.

HIPPURIS VULGARIS, Linn.

Fruits abundant. Interglacial beds, Hailes, Kilmaurs, Cowden Glen, and Airdrie. Preglacial (Cromer Forest-bed), passim.

MYRIOPHYLLUM SPICATUM, Linn.

Fruits and detached carpels. Interglacial, Kilmaurs and Cowden Glen. Preglacial (Cromer Forest-bed), Cromer, Sidestrand, and Mundesley.

TRAPA NATANS, Linn.

Well-preserved fruits. Preglacial (Cromer Forest-bed), Mundesley, Sidestrand, Ostend, and Pakefield. No trace of this species has yet been found in any later deposit in Britain.

APIUM NUDIFLORUM, Reich.

Three fruits with the carpels still attached—apparently not quite ripe. Interglacial, Airdrie, near Greenock (Bennie).

CARUM CARUI, Linn.

One well-preserved detached carpel. Interglacial, Redhall, near Edinburgh. This species is unknown from postglacial deposits, and is generally considered to occur in Britain only as an introduced plant.

OENANTHE LACHENALII, Gmelin.

Only single specimens from each locality. Postglacial (Clyde beds), Garvel Park (from Mr. Scott). Preglacial (Cromer Forest-bed), Mundesley and Pakefield.

PEUCEDANUM PALUSTRE, Mœnch.

A single well-preserved detached carpel. Preglacial (Cromer Forest-bed), Pakefield.

CORNUS SANGUINEA, Linn.

Recognised by the characteristic two-celled stones. Post-glacial (submerged peat), Albert Docks, near London (Mr. Spurrell). Preglacial (Cromer Forest-bed), Happisburgh.

SAMBUCUS NIGRA, Linn.

Several seeds from each locality. Postglacial, Southampton Docks, from peat below the sea-level (Mr. Whitaker). Postglacial, Tilbury Docks, from similar beds (Mr. Spurrell). Interglacial, Redhall, near Edinburgh (Mr. Bennie).

VALERIANA OFFICINALIS, Linn.

Nine detached fruits all rather smaller than my recent specimens, but otherwise indistinguishable. Interglacial, Redhall.

EUPATORIUM CANNABINUM, Linn.

Detached fruits. Postglacial, Tilbury Docks (Mr. Spurrell).

BIDENS CERNUA, Linn.

Fruits abundant but small. Interglacial, Redhall, near Edinburgh.

BIDENS TRIPARTITA, Linn.

Fruits very rare. Preglacial (Cromer Forest-bed), Mundesley and Kessingland.

MATRICARIA INODORA, Linn.

Thirteen well-preserved fruits. Interglacial, Redhall.

SENECIO SYLVATICUS, Linn.

Six fruits. Interglacial, Redhall.

CARDUUS LANCEOLATUS, Linn.

Several fruits. Interglacial, Redhall. Some thistle seeds from the Cromer Forest-bed perhaps also belong to this species. From both horizons the fruit are rather small for C. lanceolatus.

CARDUUS, sp.

One fruit from Redhall has a conspicuous collar, and apparently belongs to another species. It does not satisfactorily agree with any with which it has been compared, but seems nearest to *C. palustris*.

LAPSANA COMMUNIS, Linn.

Three well-preserved fruits. Interglacial, Redhall.

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LEONTODON AUTUMNALIS, Linn.

One well-preserved fruit, showing the characteristic dilated base of the pappus-hairs. Interglacial, Redhall.

TARAXACUM OFFICINALE, Web.

A few fruits with portion of the beak. Postglacial (Clyde beds), Garvel Park and Roxburgh Street, Greenock (from Mr. Thomas Scott). Interglacial, Redhall (Mr. Bennie).

Sonchus Arvensis, Linn.

Six fruits. Interglacial, Redhall.

ARCTOSTAPHYLOS UVA-URSI, Spreng.

Seeds and leaves. Bovey Tracey, Devonshire. (Nathorst, Journ. Bot. n. s. vol. ii. p. 227).

[FRAXINUS EXCELSIOR, Linn.]

Ash wood is recorded from several localities in postglacial beds, but I have not been able to obtain any specimens. The well-marked and characteristic fruit has not been found.

MENYANTHES TRIFOLIATA, Linn.

Seeds (many split by birds). Postglacial submerged peat, Montrose (Mr. J. C. Howden). Interglacial, Redhall and Airdrie. Preglacial (Cromer Forest-bed), passim.

MYOSOTIS LINGULATA, Lehm.

A few nutlets. Preglacial (Cromer Forest-bed), Beeston and Mundesley.

BARTSIA ODONTITES, Huds.

Four seeds. Postglacial (Clyde beds), Garvel Park (Mr. Thomas Scott).

PEDICULARIS PALUSTRIS, Linn.

A few seeds. Interglacial, Redhall.

LYCOPUS EUROPAEUS, Linn.

Four or five nutlets. Preglacial (Cromer Forest-bed), Mundesley.

THYMUS SERPYLLUM, Linn.

A detached calyx. Postglacial (Clyde beds), Roxburgh Street, Greenock. Mr. Thomas Scott has sent a calyx of *Thymus*, which, though it does not exactly match any of the recent specimens with which Mr. Ridley and I were able to compare it, yet seems undoubtedly to belong to this species. The calyx in the recent plant is very variable, and our fossil comes within the extreme limits.

[SCUTELLARIA GALERICULATA, Linn.]

Interglacial, Cowden Glen. Mr. Mahony records a leaf closely resembling this species ¹. The leaf of *Scutellaria* being non-deciduous and of a soft texture, it is scarcely likely to be found fossil, and in the absence of the very characteristic fruit the species ought not to be included in the list.

PRUNELLA VULGARIS, Linn.

Two nutlets, only one well-preserved. Interglacial, Redhall. Somewhat smaller than my recent specimens, but otherwise indistinguishable.

STACHYS PALUSTRIS, Linn.

Several nutlets. Interglacial, Redhall. Preglacial (Cromer Forest-bed), Beeston.

GALEOPSIS TETRAHIT, Linn.

Three nutlets. Interglacial, Redhall. This species is commonly considered to be an introduced weed of cultivation, but it was certainly native during this interglacial period. The specimens agree in every respect with the recent forms, but G. Tetrahit and G. speciosa cannot be distinguished by the fruit.

ATRIPLEX PATULA, Linn.

Numerous seeds. Postglacial (Clyde beds), Garvel Park, and Roxburgh Street, Greenock (Mr. Scott). Interglacial, Redhall. Preglacial (Cromer Forest-bed), Sidestrand and Pakefield. In the interglacial and preglacial beds only the smaller seeds of this species have been found.

¹ Geological Magazine, vol. vi. p. 306.

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SUAEDA MARITIMA, Dum.

Seeds corresponding exactly with this species, except that they are slightly smaller than my recent specimens, occur abundantly in the Cromer Forest-bed. They may, however, belong to a species of *Atriplex*.

POLYGONUM AVICULARE, Linn.

Fourteen detached fruits. Interglacial, Redhall.

POLYGONUM PERSICARIA, Linn.

Seven detached fruits. Interglacial, Redhall.

RUMEX MARITIMUS, Linn.

Fruit in fruiting sepals. Preglacial (Cromer Forest-bed), at most localities.

RUMEX OBTUSIFOLIUS, Linn.

Fruit in fruiting sepals. Interglacial, Redhall.

RUMEX CRISPUS, Linn.

Fruit in fruiting sepals, and detached nuts. Postglacial (Clyde beds), Garvel Park (Mr. Scott). Interglacial, Redhall. Preglacial (Cromer Forest-bed), Sidestrand. The Forest-bed specimen was accidentally destroyed before properly compared with the recent forms.

RUMEX ACETOSELLA, Linn.

A single well-preserved fruit. Preglacial (Cromer Forestbed), Beeston.

EUPHORBIA HELIOSCOPIA, Linn.

Eight seeds, all split lengthwise (by birds?). Interglacial Redhall.

EUPHORBIA AMYGDALOIDES, Linn.

Two seeds. Preglacial (Cromer Forest-bed), Mundesley.

ULMUS, sp.

Elm leaves are common in the preglacial Cromer Forestbed at Happisburgh. Wood has been recorded from a depth of ten feet in Digby Fen ¹.

¹ Skertchly, Memoir on the Fenland, Memoirs of the Geological Survey, 1877, p. 170.

BETULA ALBA, Linn.

Wood, leaves, and seeds. Postglacial, passim. Interglacial, Hailes and Cowden Glen. Preglacial (Cromer Forest-bed), passim.

BETULA NANA, Linn.

Leaves. A common species in beds associated with boulder clay. Postglacial, Bridlington (Nathorst), Holmpton, near Withernsea, Bovey Tracey (Heer). Interglacial, Airdrie. At base of the glacial deposits at Happisburgh in Norfolk.

ALNUS GLUTINOSA, Linn.

Cones. Postglacial, Hornsea and Sand le Meer in Holderness; submerged peat of Albert and Tilbury Docks (Mr. Spurrell). Interglacial, Hailes and Redhall. Preglacial (Cromer Forest-bed), at most localities.

CORYLUS AVELLANA, Linn.

Nuts. Postglacial, Sand le Meer in Holderness; Southampton Docks (from Mr. Whitaker); Albert Docks (from Mr. Spurrell), &c. Interglacial, Hailes and Redhall. Preglacial (Cromer Forest-bed), Ostend and Pakefield.

QUERCUS ROBUR, Linn.

Wood, leaves, and acorn-cups. Postglacial at many localities. Interglacial, Redhall. Preglacial (Cromer Forest-bed), at many localities.

CASTANEA SATIVA, Mill.

Mr. H. N. Ridley has found charcoal of this wood in a bed with palaeolithic implements between Crayford and Erith¹. This is apparently the only record of the chestnut in a fossil state in this country.

FAGUS SYLVATICA, Linn.

Leaves. Preglacial (Cromer Forest-bed), at Happisburgh.

² Journ. Bot. vol. xxiii. p. 253.

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SALIX CINEREA, Linn.

Leaves. Bovey Tracey, Devonshire (Heer and Nathorst). Preglacial (Cromer-Forest bed), (Nathorst).

SALIX REPENS, Linn.

Leaves. Postglacial, Barnwell. A number of leaves in the Woodwardian Museum (Cambridge) appear to be correctly referred to this species.

SALIX HERBACEA, Linn.

Leaves. Interglacial, Hailes.

SALIX POLARIS, Wahlb.

Leaves. Below the glacial deposits, Beeston, Mundesley, and Ostend in Norfolk (Nathorst and Reid).

Several other species of *Salix* have been recorded with doubt, but the determination from leaves is very difficult.

EMPETRUM NIGRUM, Linn.

Compressed berries and stones. Interglacial, Airdrie.

CERATOPHYLLUM DEMERSUM, Linn.

Fruit. Postglacial, Mundesley. Preglacial (Cromer Forestbed). The preglacial specimens vary much in the length of the spurs, but only one has been found entirely without them.

GYMNOSPERMAE.

TAXUS BACCATA, Linn.

Wood and seeds. Postglacial in submerged peats, &c. of the Fenland; Albert Docks (Mr. Spurrell). Preglacial (Cromer Forest-bed) at several localities.

PINUS SYLVESTRIS, Linn.

Cones, wood, and bark. Postglacial, in submerged peats of the Fenland, &c. Interglacial (bark, but no cones), Hailes, Redhall, and Cowden Glen. Preglacial (Cromer Forest-bed) at many localities (wood and cones).

PINUS ABIES, Linn.

Cones. Preglacial (Cromer Forest-bed), abundant. Unknown in later deposits in Britain.

MONOCOTYLEDONS.

Juncus, sp.

Fruit of rushes are abundant, but I cannot obtain any specimens in a determinable state. Some from Redhall and Hailes apparently belong to \mathcal{F} . glaucus.

SPARGANIUM RAMOSUM, Curtis.

Fruit. Postglacial, Garvel Park—two very small and doubtful specimens received from Mr. Scott. Interglacial, Redhall—very abundant, but small. Preglacial (Cromer Forest-bed)—abundant at Pakefield, very rare elsewhere.

ALISMA PLANTAGO, Linn.

Fruit. Interglacial, Cowden Glen. Preglacial (Cromer Forest-bed), common at various localities.

POTAMOGETON RUFESCENS, Schrad.

Drupe. Postglacial, Hoxne (Ridley and Reid.)

POTAMOGETON HETEROPHYLLUS, Schreb.

Drupes. Interglacial, Hailes. Preglacial (Cromer Forestbed), abundant at most localities.

POTAMOGETON LUCENS, Linn.

Drupes. Preglacial (Cromer Forest-bed), on the foreshore between Cromer and Runton. This species and *P. praelongus* have only been found at this one locality in the Forest-bed, the other four preglacial forms are abundant nearly everywhere.

POTAMOGETON PRAELONGUS, Wulf.

Three drupes. Preglacial (Cromer Forest-bed, between Cromer and Runton).

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POTAMOGETON PERFOLIATUS, Linn.

Drupes. Interglacial, Kilmaurs, Redhall, Hailes, and Cowden Glen.

POTAMOGETON CRISPUS, Linn.

Drupes, and occasionally spikes of fruit. Preglacial (Cromer Forest-bed), at various localities.

POTAMOGETON PUSILLUS, Linn.

Drupes. Interglacial, Redhall, Hailes, and Cowden Glen.

POTAMOGETON TRICHOIDES.

Drupes. Preglacial (Cromer Forest-bed), abundant at several localities.

POTAMOGETON PECTINATUS, Linn.

Drupes. Interglacial, Cowden Glen. Preglacial (Cromer Forest-bed), common at most localities and often very large.

ZANNICHELLIA PALUSTRIS, Linn.

Achenes. Interglacial, Kilmaurs, one specimen received from Mr. John Young. Preglacial (Cromer Forest-bed), abundant. At Pakefield a remarkably spinose form occurs.

ELEOCHARIS PALUSTRIS, R. Br.

Nuts. Interglacial, Hailes and Redhall.

SCIRPUS PAUCIFLORUS, Lightf.

Nuts. Interglacial, Redhall, Hailes, and Stair. Preglacial, at several localities.

It is not easy to distinguish S. pauciflorus from certain species of Carex, in the absence of the utricle; it is possible that some of the specimens referred to Scirpus may belong to Carex.

SCIRPUS CAESPITOSUS, Linn.

Nuts. Preglacial, abundant at various localities.

SCIRPUS FLUITANS, Linn.

Nuts. Preglacial, occasionally found at Beeston.

SCIRPUS SETACEUS, Linn.

Nuts. Interglacial, Redhall and Hailes. Previously recorded in mistake from the Cromer Forest-bed.

SCIRPUS LACUSTRIS, Linn.

Nuts. Interglacial, Hailes and Cowden Glen. Preglacial (Cromer Forest-bed), common at Beeston and Mundesley.

SCIRPUS MARITIMUS, Linn.

A single damaged nut, from peat beneath the sea-level at Southampton Docks, seems to correspond more closely with this species than with *S. lacustris*.

ERIOPHORUM ANGUSTIFOLIUM, Roth.

Portions of stem and base of the leafy bracts. Preglacial (Cromer Forest-bed), between Cromer and Runton. Several specimens showing the very characteristic bracts have lately been found. The nut of *Eriophorum* does not appear to be able to resist decay—it has not been found fossil.

CLADIUM GERMANICUM, Schrad.

The hard fruit are occasionally found in the preglacial Cromer Forest-bed at Beeston and Mundesley.

CAREX DIOICA, Linn.

Detached nuts. Postglacial (Clyde beds), Roxburgh Street, Greenock—two nuts received from Mr. Scott probably belong to this species. Interglacial, Redhall and Airdrie.

CAREX ECHINATA, Murr.

Nuts. Interglacial, Hailes and Redhall.

CAREX CANESCENS, Linn.

Nuts, retaining the pale colour. Interglacial, Redhall.

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CAREX PANICEA, Linn.

Nuts, with and without utricle. Interglacial, Redhall. Abundant.

CAREX FLAVA, Linn.

Nuts apparently belonging to this species are found in the interglacial beds at Hailes and Redhall.

CAREX PALUDOSA, Good.

Nut in utricle. Preglacial, Cromer Forest-bed, Pakefield.

CAREX RIPARIA? Curtis.

Nut in utricle. Preglacial, Cromer Forest-bed, Mundesley. A doubtful determination.

CAREX ROSTRATA, Stokes.

Nuts in utricle. Interglacial, Airdrie and Cowden Glen. Abundant.

ANTHOXANTHUM ODORATUM, Linn.

A single fruit, determined by Mr. Carruthers. Postglacial, Greenock (from Mr. Scott). The specimen looks very recent.

AGROSTIS, sp.

One seed. Interglacial, Redhall.

HOLCUS LANATUS, Linn.

Fruit, determined by Mr. Carruthers. Interglacial, Redhall.

PHRAGMITES COMMUNIS, Linn.

Portions of panicles are found in a postglacial peaty bed on Kelsey Hill near Hull. Matted stems are common in the Cromer Forest-bed.

POA TRIVIALIS, Linn.

A single fruit, determined by Mr. Carruthers. Postglacial, Greenock (from Mr. Scott). The specimen looks very recent. Another fruit from the interglacial beds of Redhall has been obtained by Mr. Bennie.

[HORDEUM DISTICHUM, Linn.]

A single fruit found at the gas-works in Montrose, in peat beneath 20 feet of estuary mud and sand. (J. C. Howden, Trans. Edin. Geol. Soc. vol. i. p. 144). Mr. Howden has kindly allowed me to examine the plants from this locality. The barley is of a brownish colour, and uncompressed. Seeds of bog-bean, said to have come out of the same bed, are mere husks, without any remains of the albumen. The peat is much compressed, and changed into a bituminous-looking lignite, while the associated wood is brown or black, and much altered. The seed of barley has all the appearance of a specimen that has been washing about in the sea for some time, but it does not appear to be fossil.

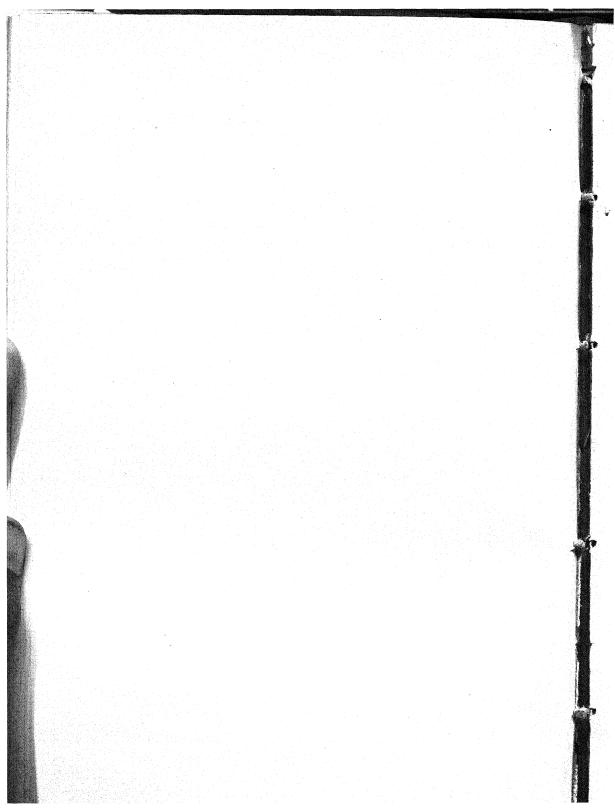
CRYPTOGAMS.

OSMUNDA REGALIS, Linn.

The woody root-stocks are common in the preglacial Cromer Forest-bed.

ISOËTES LACUSTRIS, Linn.

Macrospores, abundant. Postglacial, Garvel Park. Interglacial, Hailes, Airdrie, and Kilmaurs. Cromer Forest-bed, Beeston, one specimen.



Recent Researches on the Saprolegnieae; a Critical Abstract of Rothert's results.

BY

MARCUS M. HARTOG, D.Sc., M.A., F.R.U.I.

HE study of the spore-formation of the Saprolegnieae as a most accessible type has been renewed again and again since Strasburger's 'Cell-book' gave an impetus to cytology. Büsgen (in Pringsheim's Jahrbücher, xiii, 1882), and a little later Marshall Ward (in Quart. Journ. Micr. Soc. N.S., xxiii, 1883) elucidated the contradictory statements of older observers by showing that the zoospores were segregated in two distinct stages, interrupted by a third in which the contents of the sporange appeared uniform and homogeneous. They regarded the clear spaces between the origins (Anlagen) of the spores in the first stage as transitory cell-plates (Büsgen), or nuclear-plates (Ward), and referred the homogeneous stage to the absorption of these plates. They described the appearance of shifting vacuoles in the young spores on their second and definitive separation. Finally, Büsgen expressed the view that the substance of the transitory cell-plates of the first segregation become converted into the 'expulsive substance,' which by its supposed swelling effected the dispersion of the zoospores.

In 1884 a careful examination led me to a totally different interpretation of the facts correctly observed by my predecessors. In a paper first read at the Association Française (July 1886), and printed in extenso in the Quarterly Journal of Microscopical Science, March 1887, I was able to prove that the hypothetical cell-plates of the first segregation are merely the optical expressions of thinnings on the parietal

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layer of protoplasm left by the aggregation into the 'origins' of zoospores, or of lacunar spaces between the latter filled with cell-sap. I interpreted the homogeneous stage as consisting 'essentially in the swelling up of the protoplasm and the loss of its resistance to osmosis,' accompanied but not caused by plasmolysis; and regarded it as 'probable that the "Hautschicht" and vacuolar walls break up at this stage as continuous layers,' and that therein was the explanation of the phenomenon. I also pointed out that a contraction of the sporange can be observed at the homogeneous stage, accompanied by the excretion of a dissolved substance strongly attractive to certain bacteria.

A second part of my paper dealt with the liberation of the zoospores. I disproved by the use of reagents the existence of any swelling expulsive matter in the sporange, proved the correctness of Cornu's discovery of flagella in the sporangial zoospores of *Achlya*, and referred the liberation to the automotility of the zoospores reacting to the chemical stimulus of dissolved oxygen in aerated water.

Two other accounts have now appeared; one by Berthold incidental to his work on 'Protoplasma Mechanik,' 1886; and a paper by Ladislaus Rothert which appeared in Polish in the Proceedings of the Cracow Academy, xvii, 1887 (it was only 'in the press' in September of that year), and in German in Cohn's Beiträge for 1888. As Rothert's work is fuller than Berthold's, and in no way contradicts it, I shall only deal with the former author. It is interesting to note that all of us except Berthold began, at least, our work in the Strassburg Institut, under the stimulus and aid of the same kindly master—Anton De Bary.

Rothert's paper we may greet as affording the first full and complete account of the double segregation and homogeneous stage, worked out independently, but confirming my views so far as they went, and completing them by showing what is the real cause of the solution of continuity in 'Hautschicht' and vacuolar wall. His paper however does more than this; it affords the first complete account we have of the formation

of the zoosporange, its septum, and the tubular process through which the spores escape. On these grounds I think it is well worth abstracting to show exactly what is our present knowledge of this most interesting study; and I shall supplement this abstract by criticisms of all points on which my own work has led me to take a different view to the author's.

Rothert's work was principally conducted on three forms of *Saprolegnia* belonging to the *ferax* group. A well-chosen field is half the battle; it is very difficult in working over a group to give equal attention to each; and he has shown that these species are far more favourable than *Dictyuchus* (genus) or *Achlya*¹.

The sporangial formation begins by the slackening to final

¹ The following brief analysis of the genera may prove useful to readers:—

Saprolegnia.—Spores leaving the sporange and swarming freely, then encysting to swarm later in the 'second form.' Innovation usually growing through the empty sporange.

Leptomitus.—Resembling Saprolegnia, but with frequent strangulations on hyphæ and sporangia. As these occur also according to Cornu, in forms otherwise referable to Achlya (Achlyogeton Schenk,) and Pythium (Myzocytium Schenk), I regard them as mere habit characters, of less worth probably than the septa of Saprolegnia torulosa, which De Bary regards nevertheless as scarcely more than a form of S. ferax. Hence it is that I described ('fälschlich,' as Rothert writes) as a Saprolegnia, a form with constricted hyphæ, but with the innovations growing into the empty sporangia, and with the sexual reproduction of S. ferax.

Achlya.—Spores on their liberation assembling to encyst in a hollow sphere at the mouth of the sporange, then swarming in the second form; innovation growing out laterally at the base of the empty sporange.

Aphanomyces.—Like Achlya, but with linear sporangia containing only a single file of zoospores; innovation growing into the empty sporange.

Dictyuchus (genus).—Spores do not leave the sporange but encyst in situ, emerging only in the second form. The sporange wall often deliquesces at the maturity of the spores.

^{&#}x27;Dictyuchus-form.'—When the spores of Achlya or Saprolegnia fail to leave it at maturity they encyst within, constituting this form or dictyosporange. They either swarm ultimately in the second form or germinate in situ by emission of a hypha.

The 'first form' of zoospore is ovoid with a pair of flagella from the front (narrow end). The 'second form' is uniform with an anterior and a posterior flagellum diverging from the hilum. The existence of these two forms constitutes the phenomenon of 'diplanetism.'

arrest of the apical growth of a hypha, while protoplasm continues to stream in from the base, usually determining an ovoid enlargement; at first the thick protoplasm of the sporangial part of the hypha passes gradually into the thinner investment of the basal part; but soon the contrast is sudden and sharp. Then at this junction the granules disappear or migrate from the protoplasm so as to form a longish ring of hyaloplasma which grows at its inner circumference to finally form a transverse disk extending across the hypha from wall to wall, sharply bounded towards the basal hypha but on the sporangial side gradually passing into the granular protoplasm.

In about half-a-minute the transverse septum appears (simultaneously) at the base of the disk, at first pale ('verwaschen'), soon sharp-contoured. In favourable cases we may see that a rather broad basal section of the disk of hyaloplasma assumes a higher refraction; this gradually thins off and becomes more clearly defined and finally condenses ('sich verdichtet') into the septum; which is clearly not formed from a granular cell-plate as Strasburger states. Before this, however, a number of Pringsheim's cellulin corpuscles had accumulated about the limiting area, and fell, by the appearance of the hyaloplasma disk, into an upper and a lower group. As the upper group disappear on the completion of the hyaloplasma disk, Rothert thinks it probable that the granules, consisting of a very soluble form of cellulose, are absorbed into the disk and by their solution afford materials for the septum.

Slight modifications occur in the formation of the hyaloplasma disk according to the relative fulness or emptiness of the sporange.

We now come to the formation of the zoospores, and first of all their partial segregation, in which stage we may call them 'spore-origins' (Sporen - Anlagen). We can distinguish between (1) full sporangia which at first contain no central cavity or to which class usually belong the smaller sized ones; (2) ordinary or normal sporangia with a fairly thick parietal

investment surrounding the cell cavity or lumen [often two or three vacuoles in *Achlya*]; and (3) starved sporangia, as I have elsewhere named them, the 'inhaltsarme' of Rothert, with only a thin parietal investment of protoplasm and an immense vacuole. These differ in the processes of segregation.

In the full sporange granules gradually wander into the hyaloplasma disk which thus becomes indistinguishable. In the other forms the granular protoplasm first retracts from the disk with which it is only connected by a thin hyaline layer investing the wall and a few delicate plasmatic threads, so that the lumen is widest at the base of the sporange. Vacuoles then appear in the disk, soon enlarging and communicating with the main vacuole of the sporange. The disk then thins in the centre, and rises peripherally up the walls. The granular protoplasm again stretches down towards the septum, and finally by the wandering of granules into the hyaloplasma the latter loses its character. At the beginning of this process, the septum usually bulges towards the basal hypha, thus indicating an increase in the turgescence of the sporange. At the end of these processes the protoplasm usually shows more or less striation or flockiness, due to the uneven distribution of granules, and, in unfilled sporangia, has an uneven surface towards the lumen. The distribution of granules in the protoplasm, and of protoplasm in the sporange, gradually becomes uniform. During these stages after the formation of the septum the sporange never elongates by more than half per cent., irrespective of the concavity of the septum and the formation of the 'process,' except in Rothert's Saprolegnia, sp. 2.

The 'process' may be formed even before the septum, at the same time with the differentiation of the spore-origins, or most frequently between these two formations. It usually occupies the apex of the sporange, but may develop at any point [except the septum]. Here again hyaloplasma accumulates at a spot, bulging out the membrane; the bulging of the membrane continues with the accumulation of hyaloplasma, until a short cylinder with a nearly hemispherical top

is formed, filled with this substance. The convex terminal wall or 'cap' is duller and less sharp-contoured than the rest of the sporangial wall; its boundary not being distinct from the protoplasm on its inner side. The hyaloplasma plug soon becomes granular, except a thin layer lining the cap of the process. [The protoplasm of the apex of all growing hyphæ is hyaline; in all cases this 'hyaloplasma' shows granules on treatment with iodine.]

The segregation of the zoospores proceeds thus. In normal sporangia appear numerous splits in the protoplasmic investment, stopping just short of the cell-wall and opening into the vacuole; these appear and disappear, and finally become constant forming a honeycomb network. At first numerous plasmatic bridges connect the origins so mapped out; but most of these soon disappear; it is to the optical expression of these bridges that we must refer Büsgen's 'Körnerplatten;' this is especially clear in *Achlya*. Some protoplasm may remain long distinct from the 'origins,' apart from the continuous wall.

In full sporangia the appearance of a zigzag slit indicates the segregation of the origins in the smaller sporangia; in the larger the segregation is produced by the appearance of linear lacunæ (Spalten) which form a connected system.

In poor sporangia the segregation rather takes place by the aggregation of protoplasm in heaps, at the expense and by the thinning of the intervening part of the parietal layer. Here also plasmatic bridges may occur, and some fragments of protoplasm are left out of the schema. (In *Aphanomyces* the spore-origins appear as bulgings of the parietal layer of protoplasm, which meet and form transverse disks, joined by the intervening thin annular portions of the parietal layer.) Rothert describes these elevations as shifting, rising and flattening out for some time before becoming stable; but I feel sure that this is a misinterpretation of the gradual 'rotation' of the protoplasmic lining of the sporange as a whole, carrying the origins with it, which may also be well observed in thin 'full' sporangia of my Saprolegnia (Lep-

tomitus) corcagiensis, as in other species of Saprolegnia and Achlya.

At the period of this 'rotation' (as I hold it) there appear clear spots free from granules in the centre of each origin, near the sporangial wall; these Rothert interprets as nuclei, though he has failed to stain them. I have succeeded once in so doing in Achlya with Draper's dichroic ink, a logwood stain. In a long discussion Rothert insists on these origins being simply 'Anlagen,' and united by the uninterrupted 'Wandbeleg' of granular protoplasm; and discusses Büsgen's 'Körnerplatten,' which he shows rest on a confusion between the plasmatic threads often uniting the origins, and the fact that there is usually an accumulation of coarse granules on the whole of the convex half of the origins, a point to which I have also drawn attention.

He ascribes the errors of his predecessors to unsuitable objects for research, to the use of insufficient powers, and the influence of preconceived ideas derived from the consideration of the embryo-sac. I may mention that Dr. Büsgen has written to me that this last was actually the case with himself. Of course these facts and considerations do away with the hypothetical gelatinous 'Zwischen-substanz,' which is only the expression of the 'Wandbeleg' between the origins.

This description of the stage of preliminary segregation is essentially the same as mine, completed however by the observation of the plasmatic threads joining the 'origins,' which I have verified and accept. I have adverted to one error of interpretation in these preliminary processes.

The origins now contract, widening the interspaces and breaking most of the plasmatic threads, and at the same time become smooth on their free surfaces which before were rough and granular. In this stage Rothert has seen the 'rotation' and change of place I have before adverted to. This stage lasts at most one or two minutes, to give place to Büsgen's 'homogeneous stage,' which Rothert calls the stage of swelling up of the spores. The origins swell up, touch, and apparently

fuse, the sporange becoming clear and brighter; the septum, previously concave, becomes convex, bulging into the sporange, and the rounded cap of the process becomes flat; the sporange has lost its turgescence. Directly afterwards vacuoles appear in the protoplasm; they come and go for some time.

Closer observation of a favourable object like S. Thuretii shows that the larger granules have disappeared leaving the protoplasm finely granular; and that the fusion of the spores is not complete, they are only in contact, polyhedral and separated by fine plane spaces. In many cases however it is difficult, in some impossible to see any separation even in this species 1. In others the apparently complete fusion may be the rule, the demonstration of separation the exception. The interspaces now extend to the wall of the sporange, which has now ceased to be a single cell; the 'origins' have become spores.

Accompanying this stage is often seen a swarming of Bacteria from all parts to execute a lively dance round the wall of the sporange and at its expiration to scatter anew. On one occasion zoospores of Saprolegnia [In which period of their diplanetism? probably the second] behaved in the same way. Everything seems in favour of its being some nutritive substance that attracts the Bacteria rather than oxygen. This can only be cell-sap; and if it passes out in sufficient quantities to attract Bacteria, there must be a diminution of the volume of the sporange; probably greater than that due to the inbulging of the septum and the flattening of the process. Measurements gave a shortening of from I to 4 per cent. Taking the latter figure the reduction in volume would be 11.5 per cent., or with that due to the two septa 13 per cent. The wall, previously turgescent, now contracts with expulsion of cell-sap, and the cause of this

¹ Yet Rothert wrote in the Botanische Zeitung, 'lässt die Quellung bis zur volligen Verschmelzung gehen, was nicht richtig ist.' He sees now that I was right in my observation; and that it needed other favourable objects to obtain the correct interpretation; and I had noticed, as he admits, the incompleteness of the homogeneity in S. corcagiensis.

contraction is the complete rupture of the continuous protoplasmic investment of the walls into segments belonging to each origin. This is easily seen in poor sporangia-in optical section the protoplasmic investment can be seen to rise and divide between two origins, and go half to each. At this moment the origins (now spores) become full of minute vacuoles, which diminish in number and enlarge as the spores swell and the protoplasm becomes finely granular. 'It is here quite clear that the two processes, the vacuolation and the swelling up of the spores, go hand in hand; the phenomenon of swelling is easy to understand if we make the really obvious supposition that the protoplasm of the spores has a tendency to take up water. This could not hitherto have full play so long as the "Hautschicht," which must be regarded as continuous, hindered endosmose: but when the investment of the wall is ruptured, the "Hautschicht" is interrupted at the points of severance, and before its reconstitution cell-sap is taken up into the protoplasm of the spores and determines their swell-The cell-sap so absorbed, or a part of it, is at once excreted in the form of the shifting vacuoles 1.' I must here note that in my paper in 1886 I had pointed out that 'probably the "Hautschicht" and vacuolar wall break up at this stage and become reconstituted later on, and that herein is the true essence of the homogeneous stage,' which I had written a page above 'consists essentially in the swelling up of the protoplasm, and the loss of its resistance to osmosis.' I thus had perceived and demonstrated the essence of the homogeneity; but owing to the unfavourable type I had chiefly worked over I had failed to discover the rupture of the continuous 'Wandbeleg,' which is undoubtedly its proximate cause. The demonstration of this belongs to Rothert and I also demonstrated to Prof. De Bary and Dr. Büsgen in 1884 the loss of turgescence of the sporange, and its marked contraction, accompanied by the bacterial dance.

¹ In fact the vacuolation is really paralleled by such cases as the vacuolation of the protoplasm of a torn *Vaucheria* filament.

After this stage the lines of separation become clear, contract, and gradually round off, beginning at the angles; and as they contract they retreat from the sporange wall, which now shows a double outline. The front spore, as it retreats from the process, leaves the layer of hyaloplasma at the apex, and is only connected with it by one or two strings which are finally retracted into the spore, as the hyaloplasma from which they are drawn disappears or becomes confounded with the end wall. [My description would state that one or more vacuoles appear at the base of the hyaloplasma disk, and by their enlargement separate a terminal portion from the front spore, leaving one or two strings along which the hyaloplasma is retracted into the front spore.] Next appear the cilia, as slow outgrowths, at first short straight bristles, with simple oscillations. The front spore has its cilia always at the front end next the process; but there appears no polarity about the others. At the same time the spores manifest shaking (wackelnde) movements, increasing in strength till their discharge.

During this contraction and development of the spores, they become warty, and some of the processes are abstricted. These lumps of protoplasm after independent movements are mostly absorbed (probably always) by the very spores from which they were separated; a few may be unabsorbed, pass out with the spores and undergo diffluence; but this makes no difference to the spores themselves. Rothert recalls similar processes described by De Bary in the formation of the oospheres. The mature zoospores now contain three vacuoles, of which at least one, that at the front end, contracts rhythmically. [I have seen in *Achlya* at this stage all three vacuoles rhythmically contractile.]

On treatment with iodine about a quarter of the protoplasm turns dark brown, and contains black granules just below the surface. Nothing of this shows in the fresh state, nor is there any polar relation of the dark portion to the axis of the spore. Rothert suggests no explanation; it seems to me that we may fairly refer the browning to glycogenic contents to be used up in the formation of the cyst-wall when the spores come to rest.

The discharge of the spores occurs thus. The end wall may open in various ways. (1) The front spore presses into the process and against the cap, pushing it up into a hemisphere. The end wall gets paler and lost to view a little before it disappears. (2) The end wall disappears before the spore reaches it; discharge at once ensues. (3) In a few cases it lifted like a lid, and only disappeared after discharge was completed. (4) In cases where the end wall was unusually stiff and clearly outlined, the front spore pressed through an invisible opening, tearing to pieces in the passage; a few others followed, undergoing the same fate; but these gradually enlarged the hole so that the rest could pass through normally, but very slowly, leaving part of the end wall in sitû, which probably never disappears. In my paper I have described the first two modes of discharge; the third I have not seen; the fourth I have since observed in S. ferax (monoica).

In discharge the front zoospore, which had retreated from the process, now moves up into it; and as soon as it opens, presses out and goes on its own spontaneous motion. The others follow, at first 'stormily,' the front ones close pressed against one another; and this is sometimes the case with all; quite as often, however, the later ones move to and fro, without haste, and only find the exit after much hesitation; not infrequently do the last fail to find it, and encyst within the sporange. No change in calibre or length takes place in the sporange during this process.

11.

While this description of the formation of zoospores and the opening of the sporange is chiefly taken from *Saprolegnia*, it applies on the whole to the other species examined, including the *Achlya polyandra* of the Strassburg Laboratory.

Rothert admits that his observations on Achlya were less complete and numerous than on Saprolegnia. Here apparently he has never seen the stage of swelling result in complete homogeneity; the planes of separation persisted throughout; after this the spores, instead of contracting from

one another, retreat from the cell-wall, and cease to be clearly separated. In liberation the spore-mass forms a cylinder and presses out, becoming thinner at the outer end, and only later at the base; sometimes this column breaks up transversely into several, and finally these break up into separate spores often united by plasmatic threads; as the spores pass out they group into a hollow sphere at the mouth of the sporange.

In his 'Nachtrag' he insists strongly that my description of the liberation of the zoospores in Achlya polyandra is incorrect, and that they are not biflagellate as Cornu and I describe. This involves two points; first of all the identity of my species with A. polyandra of Hildebrand (who founded the species in Pringsheim's Jahrbücher, vii. 1867-8), and next whether I am justified in extending my observations to other species of Achlya. As to the first point, my species was identical in all characters with Hildebrand's careful diagnosis; while De Bary expresses grave doubts as to the identity of his 1. As to the second point, the behaviour of the zoospores at and after liberation in another species, which I identify with Achlya recurva, Cornu, is exactly the same as in A. polyandra. Cornu ascribes flagella to the zoospores of Achlya generally, without particularising the species; and a positive assertion of a trustworthy observer is worth all the negative evidence in the world. I have always failed to see the flagella without iodine staining; and Rothert has never definitely looked for them by staining at the stage of liberation2. We shall see later that there is independent ground for believing in their presence.

Dictyuchus clavatus was also observed by Rothert. Its processes are essentially the same as in the other genera, except that the liberation is effected by the deliquescence of the sporangial wall when the spores slowly separate a little and at once encyst. Leptomitus lacteus shows the relations of Saprolegnia in the main.

The oogonia, as seen in Achlya, show exactly the same

Beiträge zur Morph. u. Phys. d. Pilze, Ser. IV. p. 49.
 As he has informed me by letter.

processes as the sporangia: formation of oosphere 'anlagen'; development of septum; rupture of the connecting layer; swelling of the oospheres; excretion of cell-sap, as shown by a contraction of the oogonium and the assemblage of swarming Bacteria. After this swelling the oospheres (oospores Rothert terms them) contract and round off, excreting lumps of protoplasm and taking them up again. They also show the same dark granules on treatment with iodine. In position as in development zoosporangia and oogonia are homologous; which is to be developed seems rather a matter of date than anything else: a hypha cut off to-day produces the former; to-morrow or the next day it would have produced the latter; but on the whole it appears that cultures from successive generations of zoospores tend to produce oospores more readily, and recent cultures from oospores produce especially abundant crops of zoosporangia. To this I may add that cold, and drying up of the water (to a less degree), both tend to induce the early formation of the sexual fruit.

I have found in a *Saprolegnia*, which I believe to be De Bary's *S. ferax*, form *torulosa*, that small cultures drying up tended to produce spheroidal dilatations at the ends of fine hyphæ which were cut off by septa. On moistening, the contents became ordinary zoospores, and these were freed by deliquescence of the cell-wall.

In his supplement or 'Nachtrag,' Rothert first gives an abstract of Berthold's confirmatory work: and then proceeds to investigate my theory of liberation, which I ascribe in my paper 'not to any such expulsive matter as has been assumed, but to the chemical stimulus of the oxygen in the medium acting on the automotile zoospores.' He asserts that I have founded this on insufficient data, and have pushed it too far, as it cannot apply to Aphanomyces, Achlya (other than those species which Cornu and I have examined), and to Dictyuchus, for that these have no cilia. I have already shown that the probability is that flagella will everywhere be found when properly looked for in the escaping zoospores of Achlya and Aphanomyces. The genus Dictyuchus, in which the spores

only slowly roll a little apart on the deliquescence of the cell-wall, has nothing to do with the case at all; and I cannot conceive why he refers to it in this connection.

Rothert denies that in ill-aerated cultures *Dictyuchus*-forms occur owing to the zoospores failing to escape. I thought the fact notorious, and did not adduce details. Here, however, is a crucial case. The cover of a culture was luted to an air-tight cell of wood-pulp saturated with paraffin, fixed to the slide while warm. The first two zoosporangia to open discharged all their zoospores; the third discharged half, and one remained sticking in the passage; many more opened, but all their zoospores encysted in the sporange, constituting the *Dictyuchus*-form. The inference is obvious that they escape to get into purer conditions than inside the sporange; but that I pushed this evidence somewhat far in ascribing the stimulus to free oxygen is rendered probable by some experiments Rothert publishes as conclusive; they are, however, very imperfect. I shall now discuss these.

I. Water is boiled in a test-tube and quickly cooled to 24° C. by pouring cold water on the outside; a square papercell is put on the slide, filled with the boiled water, and covered with a well-fitting cover, so that the water, very poor in air, was almost completely shut off from the atmosphere; and we have reason to assume that during the observation it remained approximately free from air. Before covering, excised Saprolegnia-material with sporangia in various stages was introduced, and observed. Both development and liberation of the spores was normal, though both were much slackened; no spore remained in the sporange though they soon came to rest.

In answer to this we may note four distinct points. (1) The air is very imperfectly expelled from water by a single boil up. (2) Air is taken up on cooling, and especially in placing on the slide. (3) Slide, cover, and especially papercell, are coated with an air film which they give up to the water. (4) This poor solution of air in water is probably infinitely richer than the inside of the sporange with the active

metabolism that from all analogy we must infer goes on in the maturation of the zoospores. The experiment is not conclusive.

II. The zoospores on emission in a similar experiment are not attracted when a cleft for air is left, nor when there are air bubbles. This is quite possible according to Fechner's law; from zero to a very small quantity of air the attraction may be more marked than from a small quantity to saturation.

But I admit that my reasoning went too far in definitely ascribing the exit of the zoospores to positive aerotaxy. The facts are equally ascribable to what I may term 'negative pneumatotaxy,' or the escaping from the products of their own metabolism. Some preliminary experiments lead me to think however that carbon dioxide is not the stimulating substance.

Rothert has repeated Walz's experiments, which tended to show that liberation was due to an expulsive substance, treating the zoosporangia at the moment of liberation with syrup (twenty-five per cent. cane sugar) or glycerine. He found first that the motion of the free zoospores is arrested by these, but does not recommence on dilution, though they retained their power of germination. On the sporange the effect was peculiar and apparently irreconcilable with either theory. On adding a drop of the reagent, liberation stopped and soon recommenced; the same sequence occurred on adding a second drop, &c.; finally it stopped, not to recommence even on dilution. This is certainly conclusive against the expulsive substance; but I fail to see how it tells at all against my views, as the free zoospores are also arrested in the reagent.

Rothert has confirmed my absolute disproof of the existence of an expulsive substance; for after the arrest of liberation by the action of iodine or alcohol, on dilution no further liberation takes place. He concludes that on the whole his experiments tell rather in favour of spontaneous liberation. But he is met by the difficulty that all the reagents behave in the same way to Achlya as to Saprolegnia, while for Achlya he cannot admit the possibility of any but an expulsive mechanism.

This is obviously due to his having overlooked the cilia, and cannot weigh at all in the matter.

I may here point out that the aggregation of the spores in Achlya into a hollow head at the mouth of the sporange they have just left, appears to be due to the mutual attraction of the spores and the tendency to place themselves with their axes parallel. This is visible even in the sporange, and induces the aggregation into a cylinder or gut-shaped mass in poor sporangia, and materially interferes with their final separation. When they leave the sporange this is counterbalanced by that peculiar irritability ('negative pneumatotaxy'?) which determines their exit. This mutual attraction, which I may term adelphotaxy, can only act at a short distance; when the sporange is discharged near the margin of the hanging drop, or in a thin layer of water on a slide, we constantly see single spores escape from the mass, swim away, and encyst apart. Cases of adelphotaxy are not so rare as we might think; in the embryology of animals this form of irritability is implicitly assumed by every one. In the vegetable kingdom we find it most obvious in the Pediastreae.

This paper is not final; it is obvious that while I have shown that the liberation is due to irritability of the zoospores, and is probably induced by a chemical stimulus, we are still in the dark as to whether this stimulus is really the positive one of oxygen in the medium (aerotactic), or the negative one of the soluble products of the metabolism of the zoospores in the sporangia themselves (pneumatotactic). Moreover there are numerous processes of differentiation in Achlya which I am now studying, and which will, with the completion of my researches on the nature of the liberative stimulus, form the subject of a fresh publication.

We are indebted to Rothert for the discovery that fragments of a healthy culture of *Saprolegnia* may be cut off and will continue to thrive in the hanging drop, and are much more normal than the fly-leg cultures usually worked with. I have found garden-centipedes far more suitable for large cultures than meal-worms.



Illustrations of the Structure and Life-history of Puccinia Graminis, the Fungus causing the 'Rust' of Wheat.

BY

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With Plates XI and XII.

THE accompanying figures, in illustration of the biology of the Fungus which causes the Rust of Wheat, have been prepared in continuation of the series of illustrations of life-histories of parasitic fungi which I was commissioned to make for the Science and Art Department, South Kensington, and the first of which (on the fungus of the Potatodisease) appeared in the Quarterly Journal of Microscopical Science in 1887¹. As before, the text is only to be regarded as a description of the figures in the plates, and I have purposely avoided any reference to matters of theory, and also to several points of interest which have cropped up during the investigation.

Fig. 1 (Pl. XI) was drawn from a longitudinal section through a still green leaf of the wheat, attacked by the fungus in what is termed the *Uredo*-form. It shows the epidermis, to the left above, with a stoma in nearly median longitudinal section. Below this are several mesophyll-cells of the leaf, with their curiously sinuous outlines, and the large intercellular spaces between them; these cells contain chlorophyll-corpuscles. To the right below is part of a vascular bundle in oblique

¹ Q. J. M. S., vol. xxvii. part 3. p. 413. [Annals of Botany, Vol. II. No. VI, August 1888.]

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longitudinal section: it is already discoloured. Further details are not shown. In the intercellular spaces of the right-hand moiety of the figure are the fine septate branching hyphae of the fungus, and these are giving rise beneath the epidermis to the first series of spores, known as wredospores; all stages of development being shown, as the uredospores force up the epidermis, rupture it, and appear on the surface as the rusty streaks so hated by the farmer. (Zeiss B.)

In Fig. 2 are seen the details of development of the uredospores under a higher power. Separate branches of the septate mycelium (which contains protoplasm with scattered, oily, orange-red drops) ascend and become swollen at the tip: the tip becomes full of very dense, fine-grained protoplasm, and a septum is formed across below the swelling. The swelling enlarges, and its oil-like orange-coloured contents increase in amount: the cell-wall thickens also, and a pale central nucleus-like body is seen at a certain stage. Further enlargement follows, the orange contents increase in amount and in depth of colour, and the cell-wall becomes thicker: then regular spike-like projections are formed on the outside of the thickened cell-wall. When the spore is completely developed, as in the larger specimen above, the wall is found to be divisible into at least two evident layers, a thick outer exosporium, which is in its turn stratified into at least two layers, and a very thin endosporium. The spore is ellipsoidal in form, and has three or four rather large germ-pores at equal distances apart on a zone midway between the two ends: the germ-pores are really pits—thin circular depressions in the inner part of the endosporium and exosporium, and they serve for the emergence of the germ-tubes. Occasionally there is a thin place at the end where the spore isjoined to the stalk. (Zeiss E.)

Fig. 3 shows a series of four successive stages in the germination of the same uredospore, sown in water on glass. In a are seen two germ-tubes, emerging from opposite germpores; b, several hours later; c, later still. It will be noticed

that the granular protoplasm of the spore becomes vacuolated, and the contents pass into the germ-tube. (Zeiss E.)

Fig. 4. A longitudinal section through the leaf of a young wheat-plant, on which uredospores had been allowed to germinate for forty-eight hours. The section passed through a stoma, cutting one of the guard-cells (omitted in the drawing); through the cut guard-cell is seen the germ-tube from an uredospore which had germinated on the epidermis. The tube had formed a slight swelling over the stoma, and then entered; its end branches around one of the mesophyll-cells bounding the respiratory cavity. The nucleus of the distal guard-cell is very clearly seen. Orange-red granules are observed in the protoplasm of the germ-tube.

In Fig. 5 (Pl. XII) is a group of the *teleutospores*, obtained from a longitudinal section of the dry ripe straw of the wheat. The mycelium has now completely destroyed the cellular tissue, and its branches produce the two-celled elongated teleutospores, instead of the uredospores; specimens can be obtained with both uredospores and teleutospores arising from the same matrix. In this stage the fungus was named *Puccinia*. (Zeiss B.)

Fig. 6 shows in greater detail two of the teleutospores from the above patch. As before, each arises as a swelling at the end of a hypha; this club-shaped swelling becomes filled with dense protoplasm, and separated off from its pedicel by a septum. The young spore is then divided into two by a horizontal wall, and each of the two cells acquires a very thick hard coat, divided into several strata, as shown in the drawing. The colour also becomes much darker than before, the outer coats of the exosporium especially being siennabrown; owing to this the streaks of teleutospores on the wheatleaf appear brown or nearly black, in contradistinction to the orange-red streaks of uredospores. These teleutospores, developed in the autumn as the wheat ripens, contain oily drops in the protoplasm, and the outer shells of the exosporium are cuticularised. Unlike the thinner walled uredospores, which are developed in the summer (July) and germinate

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forthwith, these teleutospores need to be kept for some time before they will germinate. In the usual case they are scattered with the straw, and germinate in the following spring. (Zeiss E.)

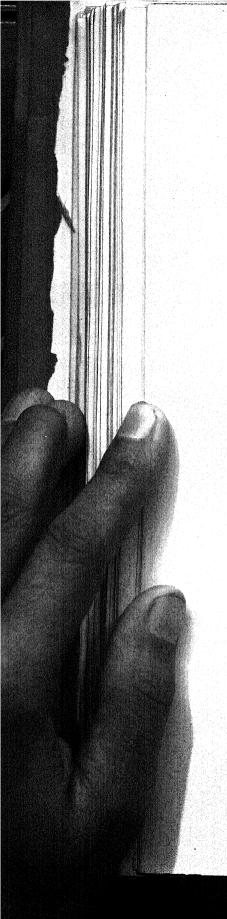
Fig. 7. Four teleutospores germinating. The one to the left and that to the right had been kept for three years in my laboratory, and germinated as seen after lying for three days in water on glass. The two middle specimens, left uncoloured, were six months old. The process of germination consists in the erosion of the thick exosporium from within, the contents enveloped by the endosporium dissolving their way through at some one point; both cells may germinate, or one only. The germ-tube grows to a short and often curved (or longer and straighter) pro-mycelium, which gradually acquires all the contents of the cell of the teleutospore, except perhaps a few granules and an oily drop or two. This pro-mycelium then becomes segmented into four or five (occasionally three) one-celled joints by transverse walls. Each cell of the promycelium then puts forth a short delicate branch, sterigma, much thinner than itself, and the tips of this sterigma slowly swells up into a spheroidal vesicle, sporidium, which takes up all or nearly all the protoplasm; occasionally the sterigma branches and more than one sporidium is formed. sporidia are very minute, as may be seen by comparing Figs. 5 and 7. All attempts to cultivate them on wheat have failed, and De Bary discovered the remarkable fact that they develop successfully only on the barberry.

Fig. 8. Three of the sporidia germinating in water on glass. (Zeiss E.)

Fig. 9. This preparation is taken from De Bary, and represents three of the sporidia germinating on the epidermis of the barberry-leaf, and sending their germ-tubes through the cuticle into the plant below. In the leaf of the barberry, the mycelium developed from these tubes ramifies between the parenchyma cells, as septate branched hyphæ, with orange-red granules in the protoplasm (see Fig. 10 a), and eventually produces the form known as Aecidium Berberidis.

Fig. 10. Transverse section of a leaf of barberry infested with the Aecidium-form. The section has passed through three spermogonia and two aecidia (to the right below). mycelium, ramifying in the mesophyll of the leaf, causes hypertrophy—due to the stimulated cells acting as centres of attraction for larger shares of food-materials, and then growing abnormally rapidly at their expense—whence the cushion-like thickening especially on the under side of the leaf. After developing in the cushion for about eighteen or twenty days, spermogonia begin to form, especially (but not only) on the upper surface. All that I can say about their earliest stages is that closely-woven balls of hyphae are formed below the epidermis, gradually become larger and hollow, and burst at the apex through the epidermis. After developing several series of spermogonia, the mycelium begins to form larger balls of interwoven hyphae beneath the epidermis of the lower side of the leaf. These gradually increase in size, and form the aecidia—hollow. spheroidal cavities filled with the aecidiospores. time the cells of the mesophyll in the neighbourhood of the aecidia are becoming disorganised: the chlorophyll-grains lose their firmness of contour, and the walls of the cells turn light brown, as shown in the figure. (Zeiss B.)

Fig. 10 a. Vertical section through an aecidium much more highly magnified. The aecidium is seen to consist of a cuplike casing of cells, peridium, with thickened and striated outer walls and orange contents, enclosing vertical series of aecidiospores developed in regular rows from the basidia below; as seen in the figure the peridium is simply formed by a modified series of cells with similar origin to the aecidiospores—all spring from a radiating series of basidia, which, again, are merely branches from the mycelium. At first the peridium forms a closed body (see Fig. 10 to the right below) beneath the epidermis; but as development proceeds the epidermis is ruptured—often at a stoma—and the peridium separates above. The aecidiospores ripen from above downwards, i.e. the older ones are ripe and separate off,

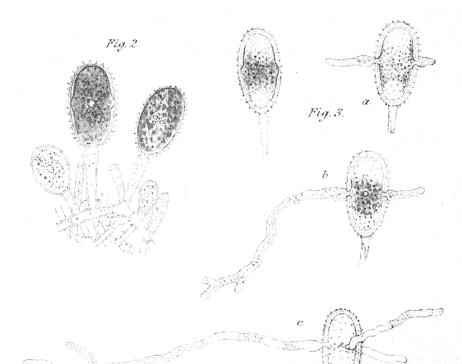


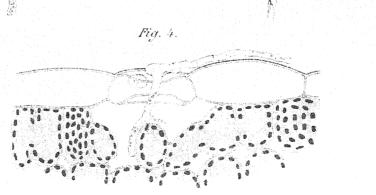
222 Marshall Ward.—Structure of Puccinia Graminis.

before the lower ones of the same series. The successive development of spores continues for some time; the young crowded spores assume polygonal shapes, but they round off as they ripen and their walls thicken. I have repeatedly examined these aecidia in the youngest stages discernible. and can find no trace of sexual organs; the search for such organs has been equally unsuccessful in aecidia of other species—e.g. those on Ranunculus and on Tussilago. The basidia clearly arise from a tufted felt of mycelium, continuous with that in the tissues of the leaf, but no definite organs of the nature of sexual organs were discovered. The aecidiospores will germinate readily in water on the leaves of the wheat, and their germ-tubes enter the stomata, and develop a mycelium which gives rise to the uredospores and eventually to the teleutospores of Puccinia Graminis. (Zeiss E.)

Fig. 11. A portion of a very thin section through a spermogonium (Zeiss E). To the right below a filament and its *spermatium* more highly magnified (Zeiss J).



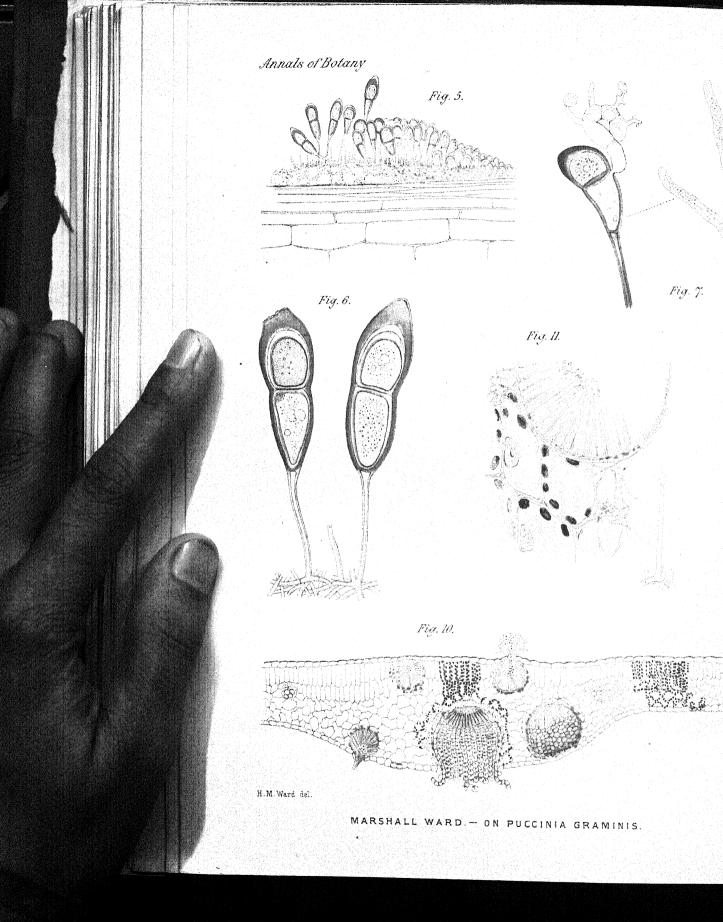




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MARSHALL WARD. - ON PUCCINIA GRAMINIS.



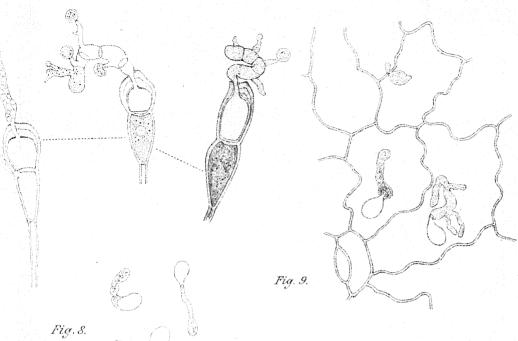
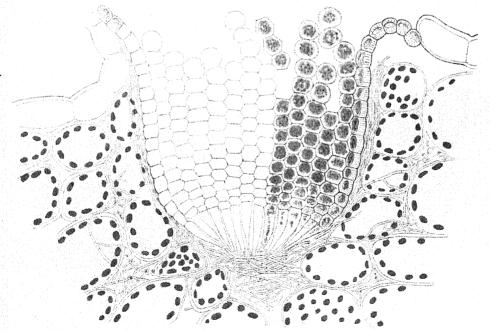
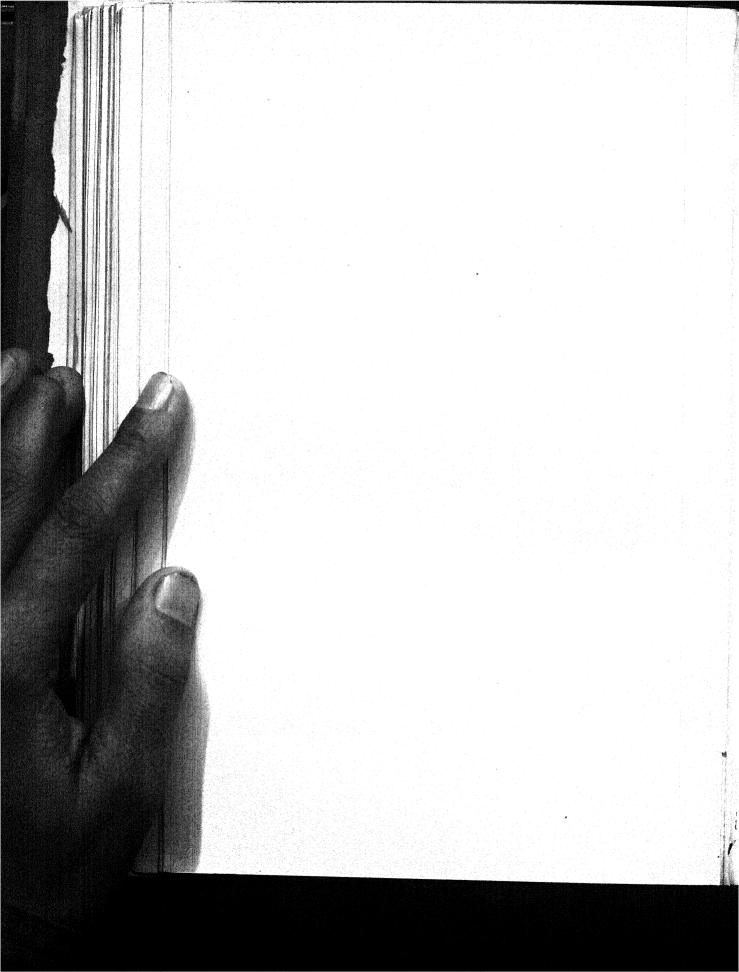


Fig. 10 a.



University Press. Oxford.



NOTES.

ON THE SYSTEMATIC POSITION OF ISOETES, I. (second note).—In my previous note on this subject (Annals, No. V) I discussed some of the principal objections which might be made to the inclusion, which I propose, of *Isoètes* among the Filicinae. But there yet remain two important morphological points to be considered, namely, the difference in the number and in the position of the sporangia on the sporophyll in *Isoètes* and in the Filicinae respectively.

Isoètes certainly resembles the Lycopodiaceae, and differs from the Filicinae, in that each sporophyll bears a single sporangium on its upper (ventral) surface, but this does not appear to be a sufficient reason for classifying this plant with the former rather than in the latter group. The relation between the Lycopodiaceae and the Filicinae in this respect is explained by Brongniart, Mettenius¹, and others, by evidence which tends to show that the single sporangium of the Lycopodiaceae corresponds to the fertile ventral segment of the leaf of the Ophioglosseae. Now it by no means follows that this reduction of a fertile leaf-segment to a single sporangium, or rather to what Prantl² terms a 'monangischer sorus,' did not take place within the limits of the Filicinae. On the contrary, if the filicinous characters of Isoètes be taken into account, it is impossible to avoid the conclusion that the reduction in question did take place within this group.

In support of this view it may be pointed out that, although there is no other case among the Filicinae of such extensive reduction, yet, as Prantl³ has shown, there are many cases of the reduction of the sorus to a single sporangium (monangischer sorus), as in Azolla (macrosporangium), Lygodium, Aneimia, Ceratopteris, and the Ophioglosseae.

¹ Mettenius, Ueber Seitenknospen bei Farnen, in Abhandl. d. k. Sächs. Ges. der Wiss., V, p. 625, Leipzig, 1861.

² Prantl, Bem. ueb. die Verwandtschaftsverhältnisse der Gefässkryptogamen, &c., in Verhandl. d. phys.-med. Ges. in Würzburg, N. F. IX, 1876.

[&]quot; Prantl, loc. cit., and Unters. zur Morphologie der Gefässkryptogamen, Heft II, Schizaeaceae, 1881.

It may be further pointed out that the dorsal position of the sporangia is not quite universal in the Filicinae. Thus, it has been ascertained that ventral, as well as dorsal, sporangia are normally borne by the sporophyll of Acrostichum (Olfersia) cervinum, and the same thing has been observed as an abnormality in various other Ferns, such as Scolopendrium vulgare, Polypodium anomalum, &c. It appears also from Goebel's researches that the sporangia of Marsilia and Pilularia are ventral.

S. H. VINES, Oxford.

ON THE OCCURRENCE OF STARCH IN THE ONION.

-The leaves of the onion are known to be somewhat exceptional in that they do not form starch in the process of assimilation, glucose, which is present in large quantities in the mesophyll-cells, apparently taking its place. Many other plants behave in a similar way, the chlorophyll-corpuscles of their leaves forming no starch in the normal process of assimilation, but by placing the plant or its leaves under unusual conditions in connection with its nutrition, starch may, in almost every case, be made to appear in larger or smaller quantities. Thus in the Musaceae, where oil might seem to take the place of starch as a product of assimilation in the mesophyll-cells, Godlewski 3 has shown that by isolating small pieces of healthy young leaves for a few hours in an atmosphere containing from six to eight per cent. of carbon dioxide, the mesophyll-cells become crowded with starch. Böhm 4 by laying the leaves in twenty per cent. sugar solution succeeded in bringing about formation of starch in a number of Monocotyledons, Galanthus, Hyacinthus, &c., in the leaves of which starch does not normally occur, but which, like the onion, contain a great deal of glucose.

He was, however, unsuccessful with the onion, both when he used a twenty per cent. sugar-solution, and in an atmosphere containing five per cent. of CO₂. Schimper ⁵, in his account of the formation and travelling of the carbohydrate in foliage-leaves, concludes that in some

¹ See Kunze, in Bot. Zeit. 1848; Moore, On some Suprasoriferous Ferns, in Journ. Linn. Soc. II, 1858; Braun, Die Frage nach der Gymnospermie der Cycadeen, in Monatsber. d. k. Akad. d. Wiss. Berlin, 1875, p. 352.

² Goebel, Entwicklungsgeschichte der Sporangien, in Bot. Zeitg., 1882, p. 776. ³ Flora, 1877, p. 215. ⁴ Bot. Zeit. 1883. ⁵ Bot. Zeit. 1885.

species of *Euphorbia* glucose is first formed and then starch from it, just as can be effected by experiment in many Liliaceae and Orchidaceae, and in the *Iris*, and he suggests that glucose is always first produced and then starch from this when the quantity of it in the cell exceeds a certain maximum, varying according to the place. He did not succeed in making the onion form starch, and says this may be due to one of two things, either,

(1) the necessary strength of glucose was not reached; or

(2) as he thinks more probable, the chlorophyll-grains of the onion have entirely lost the power of forming starch.

I have found, however, that starch can not unfrequently be detected in the elongated parenchymatous cells bordering on the vascular bundle, which, in the green part of the leaf, always contain chlorophyllcorpuscles, in fact the layer known as the 'leitscheide,' or conductingsheath.

Thus in a seedling about six-and-a-half inches long, picked at 2 P.M. on a warm sunny day, this layer contained starch, in small quantities, but at once noticeable when treated with dilute iodine solution after potash; it was found through the whole length of the leaf right down to the base, where the leaf had already begun to swell to form the future succulent leaf-scale. The green leaf of a seedling similar to the above, picked at the same time on a cold damp day, contained no starch at all. I have very rarely found small quantities in the same layer of cells in the green tubular leaf of older onions, e.g. the ordinary spring-onion whose largest leaf reaches a diameter of about a third of an inch, when the leaf has stood several hours in water after being picked. The chance of finding starch diminishes therefore as the leaf grows older. It is usually to be found in larger or smaller quantity, often in fair-sized grains in the parenchymatous cells round the vascular bundles in succulent leaf-scales of all ages, as also in the general parenchyma of the stem where the primary root and leaves come off.

In testing for starch, I followed Sachs' method of warming the sections in potash, neutralising with very dilute acetic acid, and then mounting in very dilute iodine. If this was carefully done it was seen, at any rate on the side of the bundle towards the epidermis, that the starch was contained in the chlorophyll-corpuscles.

As seedlings are evidently more in the habit of forming starch than older plants, I thought they perhaps might be induced to make a

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still larger amount, but experiments, though many times repeated, gave an almost uniformly negative result.

Thus seedlings vigorously growing in a pot were kept for several days in the sun, in a dry atmosphere (to increase transpiration) containing a much larger quantity of carbonic acid gas than normally, but only a very little starch was found in the green leaves, and that was close to the vascular bundles. A similar result was obtained in a moist atmosphere containing eight per cent. of CO₂ in the sun.

Leaves, both young and older, whole and cut up into small pieces, were fixed in damp sawdust, and placed in the sun, in an atmosphere containing about eight per cent. of CO₂, the amount found by Godlewski¹ to be most favourable to the formation of starch in leaves. These experiments lasted from several hours to several days, but the only result was, that sometimes rather more starch than usual was found in the cells adjoining the bundle on both sides; in one experiment with the first leaf of the seedling this layer was crowded with starch-grains. In the last case it might be said that the starch was simply formed from the reserve-material in the seed (which contains a good deal of oil but no starch) and was not therefore a product of assimilation, but this will not apply to the other cases mentioned, as in the majority of these the seed had been used up weeks before.

I also tried feeding with glucose and cane-sugar, both with whole plants and picked leaves,—whole and cut up in pieces—the strength of sugar-solution varying from twenty per cent. of glucose up to the syrupy glucose itself, but the result was always negative. The same was the case when the two modes of experiment were combined, i.e. feeding with sugar in an atmosphere containing eight per cent. of CO₂ in the sun. I never found any more starch than has been described above.

From the papers of Böhm, Schimper ², A. Meyer, and others, it would appear that the green leaf of the onion does not form starch at all. Schimper gives a series of *Euphorbia*-species, showing all grades between a copious formation of starch and a very scanty one (as e.g. in *E. lathyris*, where it is present almost exclusively near the vascular bundle and at the base of the leaves), and then cites as the extreme case the onion which makes no starch at all. From the above, however, it is evident that the onion is rather to be considered as an

¹ Flora, 1873, p. 378.

² Bot. Zeit. 1885, pp. 453, 456, 504.

extreme instance of a plant like Euphorbia Lathyris, since, at any rate in seedlings, starch occurs under natural conditions in the same position as in this plant. Why more copious formation of starch cannot be induced under circumstances which succeed in other cases is not evident. One of Schimper's alternative explanations, viz. that the chlorophyll-corpuscles cannot form starch, must be rejected after what has just been described, as some of them evidently can and do form starch. It is however quite consistent with the present state of our knowledge to say that the chlorophyll-corpuscles of the assimilating tissue proper of the green leaves cannot or do not form starch.

The other alternative, that it is because the solution of glucose in the cell-sap is never sufficiently concentrated, seems rather doubtful, since, in the first place, from the quantity of glucose contained in the leaves the solution is probably at least as concentrated as almost anywhere in any plant; and secondly, because in isolated leaves and pieces of leaves placed under the various conditions mentioned above, as e.g. in highly concentrated glucose solution in a warm moist atmosphere, one would imagine the cell-sap to contain a sufficiently concentrated solution of glucose, if such were the necessary condition for formation of starch.

We can only say that for some reason or reasons unknown the onion almost invariably stores up the excess of carbohydrate formed as glucose instead of in the more usual form of starch. The habit of forming starch may have been for some purpose abandoned in the course of evolution, in which case it is interesting to note that it is in the seedlings that we get an intimation of the more general process of assimilation in which starch plays so conspicuous a part.

A. B. RENDLE, Cambridge.

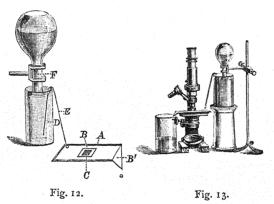
A MODIFICATION OF PAGAN'S 'GROWING SLIDE'

—In the Journal of the Quekett Microscopical Club of last year ¹ Mr. Spencer Smithson described an arrangement designed by the Rev. A. Pagan for growing on microscopical slides small organisms, such as Rotifers, Algae, &c., which live in water and require a frequent change of the medium. The results obtained with it were very remarkable; but in the original design the slide had always to be removed from the microscope and kept on a specially-constructed stage, and although in

¹ Ser. II, Vol. III, No. 18.

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many cases this is of no importance, for instance when there is no difficulty in finding again the individual which has previously been under observation, or when it is not desired to observe constantly the same individual, yet it is a very great drawback in other cases. I have therefore devised an arrangement which allows of the slide being kept constantly on the stage of the microscope and thus of the continuous observation of the same individual ¹ for weeks and even, under certain conditions to be mentioned later, for an indefinite period. Whilst it is based on the principle of Pagan's 'growing slide,' almost every detail is different in my arrangement, and its new features justify its publication. I have had it in use for the last six months, and I may say that the results which I have obtained in growing Algae were extremely satisfactory.



The arrangement which is represented on Figs. 12 and 13 requires very little explanation. Fig. 12 represents the essential parts of the apparatus. The slide, A, has the ordinary form, but is made slightly longer than the stage of the microscope, so as to project a little at both ends. On it is placed a piece of ordinary blotting paper, B, which just leaves the margins of the slide free; a hole is cut out in the centre of this paper, C, and at one end is a triangular prolongation, B', which is bent downwards close to the slide. Water is drawn from a tumbler, E, by means of a capillary tube, D, and drops on to the blotting paper. I usually make the tube just wide enough to allow a small drop of water to escape about every 20 seconds. The water is drained

¹ Of course only as long as it is in a non-mobile state.

off by the triangular prolongation of the blotting paper already mentioned. An inverted flask, F, filled with water, has its mouth just touching the surface of the water in the tumbler, E, and keeps the level of the water in the tumbler constant, thus ensuring the regular escape of drops from the capillary tube, D. The capillary tube has a thickened portion in the middle, which I find convenient to keep the tube steady. To be quite sure that the tube will work properly it is well to empty and refill it every 24 or 48 hours.

The object to be observed is placed on the slide within the central hole, C, cut in the blotting paper. It is covered with a coverslip slightly larger than the hole. The coverslip must not be put on in the usual manner, for in this way it is difficult to avoid having air-bubbles under it; but, when the paper is thoroughly saturated with water, the coverslip is placed beside the hole; it is then slid slowly over it, and the space between it and the slide is gradually filled with water.

Fig. 13, copied from a photograph taken by Mr. J. B. Farmer, and for which I am very much indebted to him, represents the apparatus in use. I may here state that the apparatus does not interfere with the drawing of an object, as the large vessel which receives the water dropping down from the blotting paper may be replaced by a very small one for some time, and thus the space on the right-hand side of the microscope is almost entirely left free.

As the water between the coverslip and the slide is in direct communication with the water in the blotting paper, which is constantly being renewed, it cannot become foul. I have never yet observed in my cultures (some of which lasted over a month) a strong growth of Bacteria, such as one would be sure to find in foul water. But in certain cases it may become desirable to have the water more rapidly renewed than is possible in the way above described. This is easily done by cutting a narrow channel (either straight or curved) from the central hole in the blotting paper to the place where the water drops down on the slide from the capillary tube. The strength of the current of water which one gets in this way may be regulated by a small piece of blotting paper which has been teased out with a needle.

With the arrangement described above it is only possible to use moderate powers (up to the combination of Zeiss' Ocular 5, Objective D). For many purposes this is quite sufficient. If higher powers are required, the paper may be removed and the object observed in the usual way, but of course it is then very difficult to continue the culture

in the case of very minute objects. In some cases I have, however, succeeded in carrying the culture a little further by proceeding in the following manner:—The hole in the blotting paper was made slightly larger than the coverslip. The latter was thus allowed to come closer down on the slide than when it was supported by the paper. The portions of the paper surrounding the hole were then teased out by means of a needle, and the teased parts were made to touch the margin of the coverslip. This was sufficient to prevent the water under the coverslip from becoming foul, and at the same time it prevented drying up. After some days, however, the water usually flooded the coverslip more or less.

When the paper has been used for about 20 days it does not allow the water to pass through very freely, and it has therefore to be renewed. This is not very easily done, but I have almost invariably succeeded by proceeding in the following manner:-First of all an excess of water is brought on the paper. As soon as the coverslip begins to float it is removed. When this is done, as much water as possible is removed from around the object with a piece of fresh blotting paper, and then the blotting paper which has been used the whole time is carefully lifted and taken off, and a new piece of exactly the same size is put down in its place. When this has become thoroughly soaked with water, the hole is again covered with a coverslip in the manner already described. During this whole process the object is almost constantly kept under observation with a low power, so that it may not be lost even if it be slightly moved. As this process may be repeated any number of times, it is obvious that a culture may be kept in operation any length of time.

To make a culture successful, it is of course necessary to adapt it as much as possible to the needs of the organism which one wants to grow. It is not my purpose to discuss this point here in detail. I wish only to point out that the supply of light and of heat has to be carefully regulated. One ought, for instance, never to forget to turn away the mirror of the microscope after observation, so that concentrated light may not fall on the object for any length of time. Special attention has also to be paid to the fact that certain organisms will only grow in certain kinds of water, &c.

In order to show what results can be attained with this arrangement, I will shortly describe my last culture, which is still in progress to-day (July 5th). On the 2nd of June a culture of *Pediastrum Bory*-

anum Menegh., var. granulatum Rabh., was begun. It produced new colonies on June 6th. One of the latter was again selected for observation, the others not being removed. Its development could be studied with the greatest ease in all its stages, and on June 25th a third generation was produced, which is now developing, although I must say it does not seem to flourish. The first generation belonged distinctly to the above-mentioned variety of P. Boryanum; its membranes were strongly 'granulated.' The second generation reached the same size as the former, and was in all respects like it, but its membranes were only slightly 'punctate.' It had therefore to be referred to the true P. Boryanum (P. Boryanum, Menegh., a. genuinum, Kirchner 1), or at least to some variety which was not the var. granulatum. It was thus shown that these two rather extreme forms belong to one and the same species, and do not even deserve to be distinguished as varieties.

If nothing else could be gained with the arrangement I have described than to show to what extent Algae vary, and thus to reduce the confusing synonymy in this branch of Botany, it should recommend itself to all those interested in its study, but it is obvious that other and more important problems may be solved by its aid.

SELMAR SCHÖNLAND, Oxford.

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¹ Kryptogamen-Flora von Schlesien. ² Bd., Erste Hälfte. Algen von Dr. Oscar Kirchner.

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The Development of Pilularia globulifera, L.

BY

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With Plates XIII. XIV. XV.

THE Pteridophytes, standing as they do between the non-vascular plants and the Phanerogams, are in many ways of especial interest to the botanist, and since the first work of Hofmeister¹ on their embryology, there has been a long series of works of greater or less value bearing upon the subject.

Owing to the imperfect methods of the earlier investigators, it was impossible to satisfactorily make out much that is rendered relatively easy by the employment of the more improved methods of to-day, this being particularly the case with the study of the early stages in the germinating spores of the heterosporous forms.

In undertaking the work, the results of which are embodied in the accompanying paper, two objects were had in view:—

1st, the investigation of the life-history of *Pilularia globulifera*; and 2nd, to determine how far the paraffin imbedding-process was of practical application in the study of vegetable embryology. In regard to the first point, the results are given at length in the following pages, and will not be recapitulated here; touching the second, it will be sufficient to say that the perfection of the sections thus obtainable, and especially the fact that series of sections can be made, will convince any one who has seen it that this method, or at any rate some method of imbedding by which similar serial sections can be made, will in future be as essential for the study of the embryology of the higher plants as it has come to be regarded in

¹ Hofmeister, Vergleichende Untersuchungen.

zoology. The old method of rendering the embryo transparent by caustic potash and similar violent agents, while it may enable one to get a general idea of the structure of an embryo, can never show with exactness the cell-arrangement in a many-celled embryo, owing to the inevitable confusion arising from trying to get optical sections where several superposed layers of cells are present. At the same time the structure of the cell-contents is absolutely destroyed by these means. With freehand sectioning it is impossible to get more than a very few sections, indeed seldom more than a single good one of a young embryo, and of course only a partial idea of its structure is thus obtainable.

Hofmeister's brief account of *Pilularia*¹, while in some particulars correct, is on the whole very imperfect, and the same may be said of Hanstein's work². The later work of Arcangeli³ is much better, but is also in several particulars, notably the development of the male prothallium and the earliest stages of the female prothallium also, far from complete, and his account of the development of the embryo, as well as the figures of the same, leave very much to be desired.

The material used in making the investigations here recorded was obtained from the botanical garden in Berlin, where, in the autumn of 1887, *Pilularia* was growing luxuriantly and had formed great numbers of ripe fruits. These were gathered at different times up to the middle of December, and placed in ordinary unglazed earthen pans filled with earth. They were kept in the cold-house connected with the laboratory, and retained their vitality perfectly as long as the observations lasted, all that was necessary being to water them moderately from time to time. In this way an abundant supply of fresh material was kept on hand all winter. It was found that if the spores were allowed to become perfectly dry for any length of time, that many of them, especially the

¹ Vergleichende Untersuchungen.

² Pilulariae globuliferae generatio cum Marsilia comparata. Bonn, 1866.

^{3 &#}x27;Sulla *Pilularia* e *Salvinia*,' in Nuovo Giornale Botanico Italiano, viii. p. 320.

macrospores, lost their power of germination. In order that the spores may germinate, it is necessary that they be brought into direct contact with water, and in order to facilitate this the fruit should be cut open, or if it has spontaneously opened, the tough membrane covering the sporangia should be partially removed. The fruit is then placed in a vessel of water, and at a temperature of from 18°-20° C. from forty to forty-eight hours is usually sufficient for the complete formation of the prothallia and sexual organs. It was found convenient, however, in many cases to retard the development, and this was readily accomplished by keeping the water at a lower temperature. In this way it is possible to so regulate the germination that all stages can be obtained, a difficult matter where the development proceeds too rapidly. With fresh material the spores germinate almost without exception.

The fruit of Pilularia globulifera, as is well known, is a round body about 3 mm. in diameter, at maturity protected by a hard dark-brown covering. It contains four chambers, each enclosing a single large sorus attached to the outer wall. The upper half of each sorus contains only microsporangia, while the lower half contains for the most part only macrosporangia, although sometimes an occasional microsporangium occurs. At maturity the fruit splits into four parts, but the sori remain covered with the brown membrane that separated the four chambers of the unopened fruit, this membrane being firm and more or less impervious to water. It was possibly a failure to remove this membrane that led Arcangeli to mistake the length of time required for the germination of the spores. If it is removed so as to allow water free access, the mucilaginous cell-walls of the sporangia absorb the water with great rapidity, and the spores are carried into the water surrounded by a soft mass of colorless jelly. Probably under natural conditions germination does not begin until the fruit has been open long enough for the covering membrane to become somewhat decayed, as the spores retain their vitality for months after the fruit is open if kept in slightly moistened earth in a cool place.

THE MICROSPORES AND MALE PROTHALLIUM.

The spores are of the tetrahedral type, and the vertical diameter is considerably less than the transverse. The three radiating ridges where the spore was formerly in contact with the other members of the tetrad are very prominent, and mark the place where the episporium and exosporium rupture when the antheridium is mature.

Arcangeli¹ succeeded in demonstrating the presence of a vegetative cell of the prothallium, but beyond this his observations were very incomplete, owing to the fact that he did not succeed in freeing the prothallium from the exosporium, but simply rendered the latter as transparent as possible. It is, however, possible to remove the exosporium entirely, and when this is done it is found that we have to do with a much more complicated structure than was supposed, and one whose development can be followed with a precision that is quite out of the question when the observations are hindered by the semi-opaque exosporium, which absolutely prevents a clear view of the interior of the spore, even when every available means is used to render it transparent. The spore contains much starch, and in the later stages it is sufficient to place the spores in a drop of water upon a glass slide and cover them with a cover-glass, and heat the slide over a flame until the water boils, when it will be found that the starch swells up sufficiently to rupture the outer coats of the spore and force out the young prothallium, surrounded only by the perfectly transparent endosporium. The prothallium is in no degree injured by this process and the dissolution of the starch is rather an advantage, as the cell-walls and nuclei are more easily studied than when the cells are filled with the opaque starch-granules.

In the earlier stages this simple process is not sufficient, and it is necessary to employ caustic potash in order to free the prothallium from the exosporium, but a very small amount must be used, and it must afterwards be thoroughly

neutralized, and the preparation washed until every trace of it is removed. Before the potash is applied the spores must be thoroughly hardened in alcohol, or better a chromic acid mixture, either a 1 per cent. watery solution, or Flemming's mixture of chromic, acetic, and osmic acids, a thorough washing being requisite after use of either of the latter. addition of the potash the slide is heated as before. prothallium is not completely set free, this can generally be accomplished by gently rubbing the cover-glass to and fro, but the potash should previously be as far as possible drawn off by means of blotting paper, and pure water run under the cover-glass. After a final washing, the preparation is neutralized with acetic or hydrochloric acid, and may then be stained with haematoxylin or some anilin color. Haematoxylin is preferable, as the preparation can then be preserved in dilute glycerine, which extracts anilin color at once or after a short time. Care must be taken with haematoxylin not to overstain, as the color deepens very much after the spores have lain in the glycerine for a short time.

According to Arcangeli¹ there are but two primary coats to the spore, the outer one showing, however, a division into three layers. The outermost of these is composed of numerous fine papillae of irregular form, and more or less anastomosing so as to form an irregular network. Within this is a layer to which these papillae are attached, and lastly the exosporium proper, which he describes as 'sottilissimo,' 'very delicate,' while in reality it is of appreciable thickness and decidedly firm and resistent. All of these three layers react like cuticularized membranes, while the endosporium proper shows the reaction of cellulose. Besides these there is often to be seen. at least in chromic acid preparations, what appears to be a loosely-fitting, nearly transparent but well-defined membrane outside, the episporium. Arcangeli assumes that all the membranes are derived from the plasma of the mother-cell, but it is more than likely that, as in the spores of Marsilia2 and in

^{1 1.} c., p. 327.

² Strasburger, Bau und Wachsthum der Zellhäute.

others more recently investigated, the episporium is derived from the epiplasma, and must therefore be regarded as an entirely independent membrane and not as a part of the exosporium.

The spore (Pl. XIII, Fig. 1) contains an easily-demonstrable nucleus, and is filled with densely granular protoplasm in which, as we have already seen, are imbedded numerous starchgranules.

The first wall formed in the germinating microspore (PLXIII, Fig. 2) is at right angles to the shorter axis of the spore, and divides it into a small basal cell and a much larger upper one, the mother-cell of the antheridium. The basal cell frequently becomes further divided into two cells of very unequal size, which represent the vegetative part of the prothallium. In the mother-cell of the antheridium there is next formed a wall which corresponds to that formed in the mother-cell of the antheridium of the Polypodiaceae. It is more or less distinctly concave above, and may be funnel-shaped, meeting the basal wall (Pl. XIII, Figs. 3, 4 m). This wall is followed by a dome-shaped wall whose base is in contact with it, but the upper part usually free and approximately concentric with the outer wall of the spore (Pl. XIII, Figs. 3, 4n), but not infrequently cases were observed where it was to a greater or less extent in contact with the endosporium, so that the cell thus formed has its wall in part made up of the endosporium (Pl. XIII. Fig. 5). This cell is the central cell of the antheridium, and from it alone are derived the mother-cells of the spermatozoids. Finally a ring-shaped wall is formed at the top, constituting the cap-cell of the antheridium. The succession of walls in the mother-cell of the antheridium, as will be seen from the above statement, follows almost exactly that of the Polypodiaceae, and shows a much less reduced state of the antheridium than was supposed to be the case; indeed occasionally the vegetative part of the male prothallium of certain Polypodiaceae (e.g. Asplenium Filix-foemina) may be reduced to a single cell 1, and

¹ D. H. Campbell, The Prothallium of Ferns, in Botanical Gazette, 1885.

the resemblance between such a reduced fern-prothallium and that of *Pilularia* is evident at a glance.

All the divisions in the central cell are by means of walls, there being no primordial cells formed as asserted by Hanstein 1 for Marsilia, and Arcangeli 2 for Pilularia. The first wall is nearly vertical, but generally more or less inclined, and divides the central cell into two nearly equal cells (Pl. XIII, Fig. 5). This stage is reached at a temperature of about 20°C., in about ten hours from the time the spores are placed in water. Each of the two cells now divides by a wall at right angles to the first and also approximately vertical, so that the young antheridium at this stage, when seen from above, shows the central cell divided into four equal parts arranged like the quadrants of a circle (Pl. XIII, Fig. 6). Each cell next divides by a horizontal wall, so that there are two strata of cells, each composed of four similar cells. The position of the succeeding walls appears to vary more or less, but in general the next wall formed in each of the eight cells seems to be generally nearly parallel to its outer wall (Pl. XIII, Fig. 10b), thus dividing it into an inner and an outer cell. Each cell now divides once more, forming altogether thirty-two cells, the number of spermcells usually formed in the completed antheridium (Pl. XIII, Fig. 11). The whole process of division occupies not far from thirty hours at a temperature of 18° to 20°C, but of course varies slightly in individual cases. The nuclei of the central cells color very intensely with haematoxylin, but those of the wall-cells of the antheridium are apparently very deficient in chromatin, to judge from the difficulty of demonstrating them satisfactorily.

As already stated, it is an easy matter to free from the exosporium the full-grown male prothallium and antheridium by simply heating. The vegetative part of the prothallium (Pl. XIII, Fig. 13) is separated by a firm wall. Above this lies the large basal cell of the antheridium, which like the vegetative

¹ Hanstein, Befruchtung und Entwicklung der Gattung *Marsilia*, in Pringsheim's Jahrbücher, iv. p. 197.

² l. c., p. 339.

cell has a small amount of granular content. The central part of the antheridium shows plainly the original bipartition, the sperm-cells being arranged in two groups. Numerous cases were observed (Fig. 9a) which looked as if sometimes a sterile cell were formed within the central cell, although this appearance may have been due to the formation of a large intercellular space. At maturity the sperm-cells are much crowded, and so nearly fill up the antheridium, that at first sight there appear to be no peripheral cells; but a careful examination shows that they are not in immediate contact with the endosporium, but are separated from it by a more or less evident space. The capcell is also somewhat difficult to detect at this stage, but just before the antheridium opens it absorbs much water, and becomes then very conspicuous (Pl. XIII, Fig. 14c). Owing to the destruction of the starch through heating, the whole prothallium appears much more transparent than in life.

The mechanism of opening seems to be the same as in other Pteridophytes. The parietal cells absorb a great deal of water, becoming in consequence very turgid. At the same time the mucilaginous walls of the ripe sperm-cells also absorb water, increasing their volume thereby, and at the same time freeing the separate cells. The tension finally becomes so great that the wall of the antheridium is ruptured and the sperm-cells are forced out. The opening usually occurs between the cap-cell and the second parietal cell. As the internal pressure is removed, the parietal cells, in case they have not been ruptured, become much distended, and in the few cases where it was possible to free the empty antheridium from the spore, the parietal cells were found to project into the cavity of the antheridium, nearly filling it. Owing to the thinness of the walls the empty antheridium usually collapses, so that it is not easy to follow the outlines of the cells.

The presence of parietal cells in the antheridium of *Pilularia* corresponds with the later investigations in regard to other heterosporous Pteridophytes. Belajeff demonstrated the

¹ Belajeff, in Bot. Zeit., 1885, pp. 793-809.

presence of such cells in the antheridia of *Isoëtes* and *Sela-ginella*, and I called attention to the same fact in *Salvinia*¹.

In the study of the development of the spermatozoids chromic acid was used as a fixing medium, and the preparations were stained with haematoxylin. After removing the prothallium from the spore, it may be carefully crushed, and the sperm-cells thus separated. The nuclei are relatively small, but contain much chromatin, so that they color very intensely. The development differs in no wise from that of other plants studied by me ².

The nucleus becomes contracted on one side so as to appear somewhat crescent-shaped (Pl. XIII, Fig. 17). It rapidly elongates, becoming at the same time thinner and more homogeneous in appearance. As it elongates it winds about the cell close to the wall in the form of a delicate spiral band, having about two complete coils (Pl. XIII, Figs. 19, 20). It occupies but a small part of the cell, the greater part being taken up with central contents, including numerous relatively large starch-granules. The cilia appear to originate from the peripheral cytoplasm, as in other forms. The sperm-cells are still clothed with a delicate membrane at the time they are expelled from the antheridium, but this is soon completely dissolved and the spermatozoids escape. These are very small, and coiled in a nearly flat spiral about the upper part of the vesicle, which is derived from the central part of the mother-cell, and contains the starch-granules which occupied that position in the sperm-cell. On killing the spermatozoid with an iodine solution the body becomes deeply colored, and the cilia are then plainly seen (Pl. XIII, Fig. 21). They are numerous, and relatively long and very delicate. Arcangeli³ states that there are but two cilia, but how he could have failed to see the others is hard to understand, as they are very easily demonstrated. The vesicle is very large, and becomes still more so by the absorption of water. Besides the starch-

¹ Campbell, in Berichte der Deutschen botanischen Gesellschaft, 1887, p. 125.

² Campbell, l. c., p. 120.

³ l. c., p. 340.

granules, it often contains others that are not colored blue by the action of iodine. It is surrounded by a very delicate membrane that in some cases shows a bluish tint when treated with iodide of potassium.

Not infrequently the spermatozoid becomes entirely free from the vesicle, and then its coils separate and the spiral becomes elongated. This is always the case with those found about the open archegonium, the vesicle being held fast in the mucilaginous matter about its opening. The spermatozoids are often held in the mucilage in which the macrospore is imbedded, so that often one sees hundreds about the macrospore, not only in the vicinity of the open archegonium, but about the whole spore. It is true that the number is greatest about the open archegonium, which frequently becomes completely choked up with them; but only one reaches the oosphere, which thereupon becomes clothed with a cell-wall so as to effectually prevent the further entrance of spermatozoids. The basal walls of the neck-cells quickly turn brown, as an indication that fertilization is effected. Under normal circumstances it seldom happens that an archegonium fails to become fertilized.

In one case free spermatozoids were observed thirty-five hours from the time the spores were placed in water, but ordinarily from five to ten hours longer were necessary.

THE MACROSPORE AND FEMALE PROTHALLIUM.

The structure of the macrospore of *Pilularia* has been so thoroughly studied, that no attempt will be made here to give more than a brief outline of the same. The spores are oval in form and white in color, quite large enough to be readily seen with the naked eye. About one-third the distance from the top is an evident constriction, above which the diameter of the spore is noticeably greater.

As already shown by the researches of Hofmeister 1, Stras-

¹ Hofmeister, Vergleichende Untersuchungen.

burger 1, Arcangeli 2, and others, the wall of the spore is very complex.

On the outside is a mucilaginous layer that swells up greatly when placed in water. Below this is a very characteristic layer, showing a prismatic structure (Pl. XIII, Fig. 23a). It is to the sudden thickening of this layer that the enlargement of the upper part of the spore is due. Within this two layers (Fig. 23. b, c) are further to be distinguished before the endosporium (a) is reached. Of these the outer is thicker and presents a punctated appearance. Sections stained with safranin, or gentian-violet, show the structure of the wall of the spore very plainly.

Owing to the mucilaginous character of the outer coat, as well as the delicate character of the spore-contents, it is quite impossible to get satisfactory sections of the fresh spore, and recourse must be had to fixing agents. Various ones were used with good results, but on the whole absolute alcohol, in which the spores should be left for two or three days at least, was found the best. A I per cent. chromic acid mixture, and Flemming's mixture of chromic, acetic and osmic acids were also successfully used, but care must be taken to thoroughly wash out the acids before further treatment.

In making the sections the spores were imbedded in paraffin, and then cut with a Cambridge rocking microtome. Schönland's methods 3, with some simplifications, were used in most cases, but in others the spores were gradually brought into clove oil, and then into xylol instead of turpentine. This method requires little time, and often gives excellent results, but is not always to be relied on, though in the early stages it answered very well, and the penetration of the paraffin was facilitated. When chromic acid mixtures were used, the specimens were brought gradually into absolute alcohol, which was then replaced by clove oil, and finally by a saturated cold solution of paraffin in turpentine before being placed in the

¹ Bau u. Wachsthum der Zellhäute.

² l. c., p. 323.

³ Bot. Centralblatt, 1887, No. 22.

melted paraffin. As a staining agent haematoxylin was used to some extent, but the best results were had with safranin and gentian-violet, the latter especially giving particularly beautiful coloring, the nuclei being much better differentiated than with the other colors ¹.

The spore is filled with protoplasm, in which are contained numerous starch-granules of various sizes, as well as oil-globules and granules of albuminous nature. The larger starch-granules are oval in form, and show more or less distinct concentric striation. Sections through the spores that have been treated with alcohol or some other fixing agent show a reticulated arrangement of the contents, and sometimes portions separate in the form of small vesicles, surrounded by a thin protoplasmic membrane. These vesicles probably represent vacuoles in the living spore. The upper part of the spore is filled with denser protoplasm, which also shows a reticulated structure, but with much finer meshes. This part (Plate XIII, Fig. 22) is almost completely free from starch-granules, and in the middle lies the nucleus, which is large and separated from the surrounding plasma by a clearly-marked membrane. It is discoid in form, strongly flattened above, and more or less undulate on the upper surface. Whether this latter peculiarity is in any way due to the reagents used cannot be determined, as it is quite impossible to make out the nucleus in the living spore. On account of its large size the nucleus is readily divided into sections in sectioning the spore, so that the interior structure is easily studied. It does not appear homogeneous (Plate XIII, Fig. 22 b), but is filled with numerous fine granules which act with reference to staining agents much like the surrounding protoplasm, and also form an indistinct net-work. The amount of chromatin is relatively very small, the chromatin-bodies being few and occupying only a very small part of the nucleus. They stain readily and deeply, the rest of the nucleus staining but little. No nucleolus was detected.

The spore, on being placed in water, begins to germinate

¹ See Moll's article on the paraffin-imbedding process in the Botanical Gazette for January, 1888.

in a very short time. The protoplasm at the top increases in volume, and begins to push out the inner spore-membranes, so that the upper part of the spore becomes decidedly more convex than at first (Plate XIII, Fig. 24). At the same time the nucleus becomes much more nearly globular, and the amount of chromatin is seen to be evidently greater, as well as to have become more evenly distributed (Plate XIII, Fig. 25). This stage was observed in sections made four-and-a-half hours after the spores were placed in water. At this time the appearance of the protoplasm in the upper part of the spore had also changed, having entirely lost the reticulated appearance which it has in the ungerminated spore.

This stage is figured by Arcangeli¹, who did not, however, recognise the true nature of the nucleus, supposing it to be the beginning of the oosphere.

The youngest stage in which it was possible to demonstrate positively the first division in the spore occurred sixteen-and-a-half hours from the commencement of germination. In this stage (Plate XIII, Figs. 26 α , b) the primary nucleus had completely divided, and a transverse wall, α , had formed, cutting off the mass of protoplasm at the top of the spore from the rest of the spore. This wall does not always have the same form, being sometimes convex above, sometimes decidedly concave. The next wall to appear is nearly parallel with the first, and is completed within three or four hours from the time the first is formed (Fig. 27, b). A few cases were observed where this second wall did not seem to have been formed, so that the central cell of the archegonium was in direct contact with the first-formed wall, but this is exceptional.

Next are formed two walls in the upper cell, nearly perpendicular to the wall b, and meeting each other so as to enclose a nearly circular central cell. When seen from above (Plate XIII, Figs. 33, 34) these walls appear nearly semicircular and concentric with the periphery of the prothallium. The nearly circular central cell is the mother-cell of the archegonium.

¹ l. c., Plate VII, Fig. 2.

The prothallium (Plate XIII, Fig. 28) now consists of four cells, the discoid basal cell, h, the two peripheral cells, $p \not p'$, and the central cell, c. As is usually the case, the mother-cell of the archegonium is distinguished from the other cells not only by its position, but also by its more densely granular protoplasm. The nucleus is also larger. It occupies the centre of the cell, and has a well-defined membrane. It is oval in form, and has chromatin-bodies of nearly round shape. A nucleolus does not seem to be present in most cases, though once a body was seen that may have been a nucleolus.

About the time that the mother-cell of the archegonium is formed, the basal cell undergoes division by a vertical wall into two nearly equal cells.

According to Arcangeli¹ there is an almost regular concentric arrangement of the cells of the basal part of the prothallium, but numerous sections failed invariably to show anything approaching his figures. The first wall (Pl. XIII, Fig. 35, 1) generally can be distinguished even after numerous divisions have taken place, and the radial walls, 2, which succeed this can also frequently be traced in the later stages, but the number of these secondary walls is so variable, and the succeeding ones so very irregular, that beyond the first three or four divisions it is quite impossible to distinguish any regular succession in the order of division.

The order, so far as it can be traced, is as follows. After the first wall (Pl. XIII, Fig. 35, 1) is formed, a number of secondary walls, 2, are formed running from the primary wall to the circumference but not strictly radial, and variable in number. The tertiary walls, 3, run from the secondary walls to the circumference, and like these are usually somewhat curved. The next series of walls are tangential, but beyond this no regular order seems to prevail. In consequence of the variable number of the secondary and tertiary walls, as well as the subsequent differences in the arrangement of cells, the resulting cell-complex is extremely irregular, and differs widely in appearance in different individuals. The marginal

¹ l. c., Plate VIII, Fig. 4.

cells undergo division by horizontal walls, but in the central part all the walls are vertical, so that the central cell of the archegonium, and later the embryo, are only separated from the cavity of the spore by a single layer of cells.

In the meantime the cells of the upper part of the prothallium have also been undergoing rapid divisions. In the peripheral cells are formed numerous radially placed vertical walls (Pl. XIII, Fig. 34), so that the central cell, seen from above, appears surrounded by a single circle of small cells. The central cell next divides by a wall parallel to its outer surface (Pl. XIII, Fig. 29), the outer cell being the mother-cell of the neck of the archegonium, the inner one giving rise to the oosphere and canal-cells. The contents of all the peripheral cells are less uniform than those in the central cell, and the nuclei are much smaller.

The development of the archegonium proceeds as follows. The mother-cell of the neck becomes divided by two cross-walls into four equal cells, and soon after the central cell has a small discoid cell, the primary canal-cell, cut off at the top (Pl. XIII, Fig. 31).

Up to this time, about thirty hours from the beginning of germination, the prothallium has increased but little in size and is still completely enclosed in the spore, and all the cells, including the central one, are very much flattened. A rapid growth in height now begins. The cells, which hitherto have been divided by vertical walls for the most part, now form horizontal walls, and at the same time increase in height, so that the young prothallium rapidly assumes its completed form. Each of the four primary neck-cells divides by a transverse septum into two, and the upper cells so formed project when full grown as a colorless papilla beyond the spore-membrane. As the neck increases in length the canal-cell elongates with it, and the ventral canal-cell is formed (Pl. XIII, Fig. 32). It was impossible to get specimens where the nuclear division was taking place, which would of course determine the matter positively, but from the relative position of the walls in the canalcells one would certainly conclude that the ventral canal-cell arises here, at any rate, not by a further division of the central cell, but by division of the primary canal-cell. The wall dividing the two canal-cells is so high up, and so much shorter than the wall by which the primary canal-cell was separated from the central cell, that it is hard to see how such changes of position could be otherwise accounted for.

The divisions in the female prothallium are usually completed in from forty to forty-five hours from the time the spores are sown, and shortly thereafter the archegonium opens and is ready for fecundation. Owing to the opacity of the covering membranes, the only part of the archegonium that can be seen in the living prothallium is the upper part of the neck. The cells of this, as in other Pteridophytes, become much distended with water and diverge widely when the neck opens, and at the same time, as has been so often observed in other Archegoniates, the contents of the disintegrated canal-cells are forced out of the opening.

Fecundation takes place very soon after the archegonium opens, the spermatozoids, as already mentioned, collecting in great numbers about the open archegonium. The opacity of the spore-membranes makes it impossible to follow the spermatozoid to the central cell, but this probably takes place very quickly owing to the shortness of the neck. In nearly every case where the spores were placed in alcohol immediately after it was supposed that fecundation had been effected, the lower neck-cells had already begun to assume the dark-brown line indicative of the fact. In these cases the two nuclei could generally be demonstrated in the germ-cell.

The oosphere becomes almost at once surrounded by a membrane which prevents the further penetration of spermatozoids. As soon as the spermatozoid enters the germ-cell it appears to go through a similar series of changes, only in reverse order, to those which the nucleus of the sperm-cell undergoes in forming the spermatozoid. In the earliest stages observed, the elongated, more or less curved form of the spermatozoid was still indicated, but the body was less homogeneous than in the free spermatozoid. The body was also

broader and shorter, indicating a separation of the chromatinmasses of which the body is composed. In all the later stages (Pl. XIII, Figs. 38–39) the spermatozoid, sp., had assumed much the appearance of an ordinary nucleus, nearly round in shape, and in close contact with the nucleus of the oosphere. The actual fusion of the two nuclei was not observed, but there is no reason to doubt that, as in other cases observed, the cavities of the two nuclei are thrown into direct communication, and that the contents of the male nucleus flow into the cavity of the female nucleus, thus completing the act of fecundation.

The nucleus of the oosphere (Pl. XIII, Figs. 38-39) is large and has a well-marked membrane, but although a membrane may be present in the male nucleus, it is certainly much less evident, and it is by no means improbable, that a definite membrane is not developed.

The upper part of the oosphere, about one-third (Pl. XIII, Fig. 38), is nearly transparent, and constitutes the so-called receptive spot. This is traversed by what look like continuations of the granular protoplasm of the lower part of the oosphere. The nucleus at this stage presents the appearance of a transparent vesicle, containing a faintly-marked net-work of fine filaments which do not stain readily, and a small amount of chromatin.

How long after the union of the two nuclei the first division in the fertilized germ-cell takes place could not be exactly determined, but it is probably within two or three hours, and possibly even sooner. In one case the germ-cell was observed undergoing division. In this instance (Pl. XIV, Fig. 1) the daughter-nuclei were already complete, but the cell-wall was not yet complete. The nuclear spindle was still very evident, and in the middle lay the cell-plate, showing plainly the separate elements of which it was composed.

If for any reason the germ-cell fails to become fecundated the prothallium may continue to grow for some time, but this

¹ Strasburger, Ueber Kern und Zelltheilung im Pflanzenreiche, 1888, pp. 225-449.

is by no means invariably the case. In no case, however, are new archegonia developed. Arcangeli's statement 1 that the chlorophyll is developed independently of the action of light was confirmed. Spores were placed in water and removed at once to a dark place, where they were allowed to remain undisturbed for a week. At the end of this time young plants were found developed in a perfectly normal manner. They were slightly smaller, and the amount of chlorophyll may have been possibly rather less than in plants grown under normal conditions, but the difference was very slight.

THE EMBRYO.

The fertilized oosphere is not perfectly spherical, but more or less elongated transversely, and before the first division is completed this is strongly marked (Pl. XIV, Figs. 1, 2). The first wall (basal wall) in the young embryo is approximately parallel to the axis of the archegonium, and divides the germcell into two equal cells (Pl. XIV, Fig. 2). The youngest case where the completed division was seen was forty-six hours after the commencement of germination, but it is not improbable that it may occur somewhat earlier, as embryos only two hours older were observed in some cases (Pl. XIV, Figs. 6–8) to be already divided into numerous cells.

Of the two primary cells, one, as in the Polypodiaceae, gives rise to the first leaf and stem, the other to the root and foot. Of course, as the structure of the prothallium is radial, it is impossible to speak of an anterior and posterior cell at this stage.

The second or quadrant-wall (Pl. XIV, Fig. 3 II) follows as in other Pteridophytes, and divides the embryo into quadrants, the two upper being as a rule evidently larger than the lower ones.

In regard to the following divisions there is much difference of opinion, at least for *Marsilia*, which probably does not differ materially from *Pilularia*. Hanstein claims that the first wall in the embryo separates at once the stem and root, and that

the subsequent divisions are to be looked upon as segments of these primary organs. Leitgeb and Arcangeli assert on the other hand that there is a regular formation of octants. My own observations do not confirm either view, but indicate that the quadrant-wall was the one which separated the primary organs, and that the quadrants are of equal morphological importance. In regard to the formation of octant-walls, while they are formed in the anterior quadrants, the corresponding walls in the root- and foot-quadrants form very unequal angles with the basal wall, so that the resulting cells are of unequal size. From this fact (see Pl. XIV, Figs. 5, 6), it is possible to distinguish the primary organs of the embryo as soon as these walls are formed.

In order to avoid confusion it will be best perhaps to take up each quadrant separately and follow its development in detail.

THE LEAF.

The leaf-quadrant, as already stated, undergoes division by an octant-wall into two entirely similar cells. Each octant now divides by a curved wall (Pl. XIV, Figs. 4-5), meeting basal and octant walls so as to form two cells, one retaining much the same form as the octant, that is tetrahedral, and appearing in section triangular; the other quadrilateral, as seen in section. The two tetrahedral cells function for a short time as apical cells, forming three series of segments corresponding to their lateral faces. Each segment next divides into an outer and an inner cell, from the former of which is derived the epidermis, from the other the ground-tissue and the vascular bundle. Sooner or later this apical growth ceases, and the growth is confined to the basal part of the leaf. The cessation of apical growth occurs about the fourth day, and before this the leaf begins to elongate (Pl. XIV, Fig. 16 a). Not infrequently one of the cells persists longer than the others, and can be detected after the leaf has assumed its conical form and become noticeably larger than the other members of the embryo (Pl. XIV, Fig. 15). In such cases the

succession of the segments may be traced with little difficulty, whereas when no definite apical cell is present (e.g. Pl. XIV, Fig. 17 a), no such arrangement of the cells is distinguishable. The obliteration of the apical cell as such is brought about by a wall parallel to its outer face. The outer cell divides by vertical walls, soon becoming indistinguishable from the other epidermal cells, and the inner cell also dividing becomes part of the ground tissue of the leaf. About the end of the fourth day the leaf begins to grow much faster than the other members and from this time onwards elongates with great rapidity. By the fifth day the differentiation of the future tissues is clearly indicated. A longitudinal section of the leaf at this stage (Pl. XIV, Figs. 17 a, b) shows on the outside a single layer of nearly cubical cells, especially wellmarked near the apex of the leaf, which is somewhat pointed. This layer of cells constitutes the primary epidermis. Beneath it are usually about two layers of cells arranged in nearly straight rows, which converge towards the apex of the leaf. These cells give rise to the mesophyll, and at an early stage large intercellular spaces are formed between them. Within these is a conical mass of cells, the outer ones of which differ but little from those lying outside them, but the innermost ones have undergone division by longitudinal walls forming the beginning of the procambium of the future vascular bundle. This longitudinal division ceases at some distance from the point of the leaf, and in consequence the vascular bundle does not extend into it. The cells of the leaf-tip above the point where the procambium ceases increase enormously in size, elongating to many times their original length, and forming thus a very loose large-celled parenchyma that ultimately dies away. From this time the growth of the leaf is due entirely to the activity of the basal part. If we examine somewhat older embryos (Pl. XIV, Figs. 22, 23) the differentiation of the young tissues is still more evident, and the limit between the actively dividing basal cells and the tip of the leaf is very conspicuous. If the base of the leaf of such an embryo as that figured in Fig. 23 is examined, it is usually

found to be decidedly convex above, in consequence of more active growth on the upper side, and the young ground-tissue is much more strongly developed than on the ventral side, where there was but a single layer of cells separating the young epidermis from the young vascular bundle. The inner procambium-cells at this stage have increased considerably in length, and begin to show the pointed ends characteristic of the elements of the mature bundle, but no tracheids are yet distinguishable, these appearing first about the ninth day.

THE ROOT-QUADRANT.

The first wall in the root-quadrant (Pl. XIV, Fig. 5) forms an angle of about 60° with the basal wall, and thus divides the quadrant into two unequal tetrahedral cells. The larger of the two is the future apical cell of the root, and from the first it forms regular series of segments, but at the beginning only the lateral faces give rise to segments, that is, three series only are developed, the first segment of the root-cap being cut off only after about two complete sets of lateral segments have been formed (Pl. XIV, Figs. 12-16 a). The apical cell of the root is from the first very conspicuous, and immediately recognizable as such. By the fourth day there have been two segments cut off from each lateral face of the apical cell, and the first segment of the root-cap has also appeared. The celldivision in the segments is very regular, and corresponds with what has been observed in other Pteridophytes. The first wall in the lateral segment (Pl. XIV, Fig. 20, I, II) is perpendicular to the broad faces of the tabular segment, and divides it into two nearly, but not quite, equal cells, as the wall does not extend quite to the centre, but meets one of the lateral walls a short distance above it. Each of the cells thus formed next divides by a tangential wall into an inner and an outer cell, the former giving rise to the cells of the plerome-cylinder, the latter to the epidermis and periblem.

An excellent idea of the succession of the divisions can be had by making a series of cross-sections through the tip of the

root, but this is best done after the root has attained some length. Part of such a series is shown in Plate XV, Figs. 2–5, taken from an embryo of nine days. The younger segments, as will be seen on comparing them with those from a younger embryo (Pl. XIV, Figs. 20, 21), are much the same, but as the sections are made further from the tip of the root changes are observed which had not yet appeared in the younger embryo. The outer of the two original cells of each semi-segment divides by a tangential wall into two nearly equal cells, and these ultimately undergo further division by similar walls, the outer into two, the inner into three.

About the time that these cells are formed (Pl. XV, Fig. 3), intercellular spaces appear at the points where the inner and outer cells are in contact, and these appear larger and larger as the root increases in diameter. The two outermost lavers. i.e. epidermis and hypoderma, undergo further radial divisions and form an uninterrupted double layer of cells, but the three original cells lying between the hypoderma and the pleromecylinder divide subsequently only by horizontal walls and form single rows of cells separating the large intercellular spaces. The older sections (Pl. XV, Figs. 4, 5) show a perfectly uniform radial structure. In the centre is a group of about nine cells. the young bundle, from which radiate at regular distances rows of three cells each. The lower cells of these rows are in contact and constitute the bundle-sheath, but the others are separated by the large intercellular spaces. Bounding the section are the two rows of cells forming epidermis and hypoderma.

The cell-division in the cap-segments is illustrated in Pl. XV, Fig. 2 a, b. In Fig. 2 b the central part shows the youngest cap-segment, the peripheral cells belonging to the next oldest segment. As seen here each segment-cell has divided into two nearly equal parts, and these, by walls at right angles to the first, also into approximately equal cells. These are next divided by tangential walls and the resulting marginal cells by radial walls, so that on section four central cells and a marginal circle of smaller ones are now visible (Fig. 2 a). These marginal cells later undergo further

divisions, but only in two planes, there never being any horizontal walls formed, so that the segments of the root-cap form single layers of cells, and its stratified structure as seen in longitudinal section is very marked.

THE STEM-QUADRANT.

The stem quadrant, like that of the leaf, divides first by a regular octant-wall, and the resulting octants grow for a time in the same way. As in the root, the apical cells are distinguishable from the first, each octant in fact functioning as such from the beginning, and dividing by segments cut off in regular order from the three inner faces of the octant, which has the tetrahedral form that characterizes the apical cell of the older stem. The first wall in each octant (Pl. XIV, Fig. 11 y) meets octant- and quadrant-walls, and cuts off a large cell which is in contact with the foot, and according to Hanstein and Arcangeli is to be regarded as part of the foot. That physiologically this is the case is indisputable, as these cells, lying as they do next the basal cells of the prothallium, must help to absorb the nutriment from the spore. As, however, these segments are cut off from the stem-quadrant, and not from the foot itself, and are in all essential particulars both in regard to form and methods of division like the later segments, it seems more in accordance with the facts to regard these segments, morphologically at least, as the first segments of the stem and second leaf, and the equivalent of the later ones.

Hanstein's statement that the first wall in the stem-quadrant of *Marsilia* corresponds to the wall in the accompanying figures, and that the octant-wall is formed subsequently, is not confirmed by later observers, nor was it found to occur in any instance observed by me in *Pilularia*.

Of the two octants, one becomes the stem and the other the second leaf, corresponding with the earlier observations of Hanstein and Arcangeli. These are often not to be distinguished from each other for some time, but as a rule the

divisions in the leaf-octant are less regular, and very often the apical cell becomes obliterated at an early period (Pl. XIV, Fig. 16c).

There seems to be no rule as to which of the octants of the stem-quadrant forms the apical cell of the stem, as it was found in about an equal number of cases to be right or left. The succession of segments cut off from the apical cell proceeds from the outside towards the octant-wall, the three segments of each series being respectively approximately parallel to the quadrant-, basal, and octant-walls. The direction of the leaf-spiral, which depends upon the arrangement of the segments, will of course be determined by the position of the original stem-octant with reference to the octant-wall. Kny 1 comes to similar conclusions with reference to the establishment of the leaf-spiral in *Ceratopteris*.

Each segment divides by a tangential wall into an inner and outer cell, the former dividing again by a similar wall and the latter by a radial wall, so that a vertical section through the young segment at this stage (Pl. XIV, Fig. 18) shows four cells, two inner and two outer ones. The inner cells undergo repeated division in all directions, but the outer ones only by radial walls.

The stem grows very slowly at first, and by the time the first leaf and root have attained length enough to break through the prothallium, the stem shows only about two completed series of segments. Even at this stage (Pl. XIV. Fig. 23) the inner cells of the segments have rapidly divided and the first traces of the vascular bundle are distinguishable.

The first segments are larger than the succeeding ones, and the broadly tetrahedral form of the original octant is thus rapidly reduced to the much narrower form of the apical cell of the older stem.

The octant which does not become the apical cell of the stem, forms, as we have seen, the second leaf of the plant. In a certain sense, assuming that the quadrant-wall establishes

¹ Kny, Die Entwicklung der Parkeriaceen, in Nova Acta Acad. Leopold. xxxvii, No. 4, p. 58.

the primary members of the embryo, we may say that the second leaf originates like the later ones, as a segment of the apical cell of the stem. Like the stem, it grows slowly at first, and in case the apical cell persists, is scarcely to be distinguished from it (Pl. XIV, Fig. 22 d, l^2). About the eighth day, however, it begins to elongate, though much more slowly than the primary leaf, and from this time onwards is very easily recognised (Pl. XIV, Fig. 25; Pl. XV, Figs. 1, 8). About two weeks after sowing the spores the second leaf begins to grow rapidly, and in a very few days reaches its full size.

THE FOOT-QUADRANT.

The first divisions in the foot-quadrant (Pl. XIV, Figs. 8, 9, &c.) follow closely those of the root, but this regularity soon ceases, and after the first two or three divisions no definite succession of the walls can be distinguished. The foot never attains any great size, and as already said, all the lower cells of the embryo probably absorb the nutriment from the spore.

As the embryo grows the prothallium keeps pace with it for some time. About the time the embryo is divided into eight cells, the upper part of the archegonium has its cells divided by tangential walls, so that this part of the embryo is surrounded by a double layer of cells (Pl. XIV, Figs. 10, 13). Both Hofmeister and Arcangeli 1 figure this condition in the unfertilized archegonium, which in *Pilularia* never occurs.

The basal cells of the prothallium divide further and develop numerous root-hairs. The plasma in the upper part of the spore increases in quantity as the embryo develops and pushes up the base of the prothallium and embryo, which become in consequence strongly concave below (Pl. XIV, Fig. 23). Although the nucleus was not observed in actual division, in a number of instances in the later stages of development bodies which behaved with reference to staining agents in the same way as nuclei were seen in this plasma-mass, and were quite probably derivations of the original 'endosperm nucleus.'

¹ l. c., Plate VIII, Fig. 5.

THE STRUCTURE AND DIVISION OF THE NUCLEI IN THE EMBRYO.

Owing to their small size the nuclei of the embryo are not well adapted for the study of nuclear division. Except during the actual division the nuclear membrane is well defined. With safranin, or better with gentian-violet, the chromatin stains very intensely, the same treatment being used as recommended by Moll for the root-tips of Phanerogams 1. In the actively growing embryo all stages of division may be found. As elsewhere, the amount of chromatin increases very perceptibly at the time of division, the resting nucleus showing but a small amount of chromatin, and the chromatin-masses being extremely small and scattered. A small nucleolus can generally be seen. A stage was observed (Pl. XIV, Fig. 28) which was not thoroughly understood. Apparently a single relatively large and intensely coloured body was present. This was so small in some cases as to be readily taken for a nucleolus, but usually it was larger, and when sufficiently magnified did not appear perfectly homogeneous; all intermediate forms between this and others where numerous chromatin-masses were present could be readily found, and led to the conclusion that the apparently single mass is in reality composed of closely apposed, but not united chromatin-bodies, which subsequently separate more widely previous to the division of the nucleus. The chromatin-bodies are short, and with ordinary lenses appear like round granules, but when more strongly magnified are seen to be somewhat elongated.

After they have completely separated a nuclear spindle is formed, the nuclear membrane having disappeared, and the division proceeds in the usual manner. The segments now undergo division, as is indicated by the evidently greater number of segments forming the nuclear plate (Pl. XIV, Fig. 29 a), but owing to their extreme minuteness it is quite impossible to make an exact computation of their number.

¹ l. c. on page 244.

SUBSEQUENT GROWTH OF THE YOUNG PLANT.

After the eighth day the first leaf grows with great rapidity, and soon reaches its full size, breaking through the overlying prothallium-cells about the ninth day. All the cells elongate very much, and in the ground-tissue are developed large intercellular spaces forming air-passages very similar to those in the root, but less systematically disposed. They are separated by single layers of cells, radially disposed, so that a crosssection (Plate XV, Fig. 6) presents the same wheel-shaped appearance that is observed in a similar section of the root. Small intercellular spaces are also formed later between the outer cells of the hypoderma. There is only one vascular bundle, and this is of a very simple character. It is surrounded by a bundle-sheath of small cells, whose walls color more intensely than those of the mesophyll. The rest of the bundle is composed of narrow cells, with more or less pointed ends, and no intercellular spaces. At two or three points are developed small spirally-marked tracheids, which are the first to be developed in the young plant. The first signs of the thickenings in their walls is evident about the ninth day, that is, about the time that the young plant breaks through the prothallium.

The epidermis consists, as is usual in leaves of this form, of very much elongated cells. As in ferns, there is some chlorophyll formed in the epidermal cells. The stomata (Plate XV, Figs. 12, 13) are few in number and of simple structure.

The second leaf (Plate XV, Fig. 8), and the succeeding ones, exhibit perhaps more frequently than the first the growth by an apical cell. This develops three series of segments, each of which divides first into an inner and an outer cell, the first forming the young epidermis, the other the mesophyll and vascular bundle, which develop in the same way as in the first leaf.

About the time that the first tracheal tissue is distinguishable, the second root is formed at the base and on the under side of the first leaf. The apical cell is formed at some distance below the surface, and the root begins to grow at

once by means of segments cut off from it in the same way as the primary root. The first trace of the vascular bundle is formed at a point in immediate contact with that of the leaf (Plate XV, Fig. 7), and its development proceeds from this point toward the apex of the young root.

The apex of the stem grows slowly, producing from time to time a complete set of segments in rapid succession, and then resting for some time before another set is formed, so that there is always considerable difference in the ages of any two succeeding sets of segments; and as the segments divide rapidly after being formed, if the apex of an older plant is examined (Pl. XV, Fig. 9), while the youngest set of segments may be perfectly plain, it is not easy to trace the limits of the older ones. From the slowness with which new segments are formed, and the crowded manner in which the young leaves are arranged, it is probable that each segment gives rise to a leaf, or rather that the two dorsal segments of each set form leaves, while the third, or ventral segment, gives rise to a root, at least the regular occurrence of roots in relatively the same position to the apical cell of the stem, as the young leaves would indicate that this is the case (Pl. XV, Fig. 9 r). All the roots however cannot be thus formed, as their number exceeds that of the leaves, and it is highly probable that the others originate from the bases of the leaves in the same way as the second root.

Owing to the rapid growth of the young leaves, and the slowness of that of the apex of the stem, the latter becomes more and more sunk, until after three or four leaves are completely grown it scarcely projects at all. The younger portions of the stem and leaves are more or less covered with short-jointed hairs, which also covered the growing-point of the stem to a certain extent. The elongation of the stem is due almost entirely to intercalary growth of the older segments.

The first leaves show scarcely a trace of the coiling that characterizes the young leaves formed later, but this becomes more and more evident as the plant grows.

THE RELATIONSHIPS OF THE MARSILIACEAE.

Botanists have long recognized the evident relationship of the Marsiliaceae to the true ferns, especially to the Polypodiaceae, and this view is strengthened by the very great resemblance in the structure of the antheridium. Whether a more complete knowledge of Salviniaceae will show further relationships between them and the Marsiliaceae is doubtful, for apart from both families being heterosporous, they have little in common.

In conclusion I beg to express my sincere thanks to Professor Kny, in whose laboratory the investigations were made, both for his valuable assistance and also for the great interest he has taken in the work from the time it was begun.

BERLIN, June, 1888.

EXPLANATION OF FIGURES IN PLATES XIII, XIV, AND XV.

Illustrating Mr. Douglas H. Campbell's paper on the Development of *Pilularia globulifera*, L.

PLATE XIII.

Figs. 1-11. Successive stages in the development of the male prothallium and antheridium of *Pilularia globulifera*. Figs. 4 c, 6, 7, and 10 b are seen from above; the others are optical longitudinal sections. Fig. 7 is from a preparation fixed with Flemming's mixture, the others are chromic acid-preparations. All were stained with haematoxylin and mounted in dilute glycerine. x, the second cell of the prothallium. \times 375.

Figs. 12, 13. Ripe antheridia removed from the spore by heating. Fig. 12 stained with haematoxylin and mounted in glycerine; Fig. 13 uncolored and examined in water. \times 375.

Fig. 14. A living microspore which is on the point of discharging the spermatozoids. c, the cap-cell of the antheridium distended with the water it has absorbed. \times 375.

Fig. 75. A partially emptied antheridium removed from the spore by heating. \times 375.

Figs. 16-20. Successive stages in the development of the spermatozoids. Chromic acid-haematoxylin-preparation. The starch-granules have been mostly destroyed by heating, but in Fig. 20 traces of them are still to be seen. Leitz oil-immersion, $\frac{1}{10}$.

Fig. 21. Free spermatozoids, a from above, b from the side; colored with iodide of potassium. a, the vesicle with the included starch-grains. a, alcohol-gentian-violet-preparation. a, a vesicle from which the spermatozoid has become free. Leitz oil-immersion, $\frac{1}{12}$.

Fig. 22. a, Longitudinal section through an ungerminated macrospore. \times 90. b, The nucleus of the same examined with a $^{1}_{6}$ oil-immersion. Alcohol-gentian-violet-preparation.

Fig. 23. A section through the wall of the macrospore. × 300. Alcohol-safranin-preparation.

Fig. 24. Longitudinal section through a macrospore 4½ hours after being placed in water. Flemming's mixture-haematoxylin-preparation.

Fig. 25. The nucleus of a spore of the same age, but colored with safranin and examined with a $\frac{1}{10}$ oil-immersion.

Fig. 26. Two sections through a spore 16½ hours after the commencement of germination, x about 100. Alcohol-haematoxylin-preparation.

Fig. 27. The first wall is completely formed. In α is shown the nucleus of the mother-cell of the prothallium, in b that of the spore.

Figs. 27-32. Successive stages in the development of the female prothallium and archegonium, × 300. a, the first wall. b, the second wall. c, the primary canal-cell. Figs. 27, 31, 32, alcohol-gentian-violet-preparations; Fig. 28, alcohol-safranin; Fig. 29, Flemming's mixture-safranin; Fig. 30, chromic acid-safranin. Fig. 27, 19½ hours; Fig. 32, 41½ hours from the beginning of germination.

Fig. 33. Cross-section of a prothallium 24 hours old. c, mother-cell of the archegonium. p, p', peripheral cells. Alcohol-gentian-violet-preparation. \times 300.

Fig. 34. A similar section to Fig. 33, but somewhat further advanced.

Fig. 35. Cross-section of the basal part of a young prothallium. The succession of the walls is indicated by the numbers. Alcohol-gentian-violet-preparation. × 300.

Fig. 36. A similar section from a full-grown prothallium. Alcohol-Bismarck-brown-preparation.

Fig. 37. A section through the neck of a full-grown archegonium. Alcohol-Bismarck-brown-preparation. \times 300.

Figs. 38, 39. Sections through archegonia in which fertilization has recently taken place. Fig. 38 a longitudinal, Fig. 39 cross-section. 52, the male nucleus. In Fig. 38 several spermatozoids are seen about the neck of the archegonium. Alcohol-gentian-violet-preparation. × 300.

PLATE XIV.

Fig. r. Transverse section of the fertilized germ-cell undergoing the first division. Alcohol-safranin-preparation. $\,\times$ 300.

Fig. 2. Longitudinal section of a somewhat more advanced stage, in which the first division is complete. This and the succeeding figures, unless otherwise stated, were drawn from preparations fixed with absolute alcohol, and colored with gentian-violet, and magnified 300 diameters.

Fig. 3. Vertical section through an embryo composed of four cells. The first wall (basal wall) is here and in the succeeding figures indicated by the number 1, the second (quadrant-wall) by 11. The direction of the arrow indicates the anterior end of the embryo.

Fig. 4 vertical, Fig. 5 transverse section through somewhat older embryo. Fig. 4, alcohol-borax-carmine-preparation. Fig. 5, alcohol-safranin-preparation.

Figs. 6-8. A series of three transverse sections through a very advanced embryo 48 hours after sowing the spores. l, leaf-quadrant; r, root; s, stem; f, foot.

Fig. 9. Series of four vertical sections through an embryo three days from the commencement of germination.

Figs. 10, 11. Two vertical sections through an embryo of four days 1.

Fig. 12. A similar section, but showing better the apical cell of the root.

Fig. 13. Median transverse section through an embryo of four days.

Fig. 14. Two other sections of the same embryo. a, above; b, below the quadrant-wall.

Fig. 16. Three transverse sections of an embryo of four days, but somewhat further advanced. The apical cell of the root has already formed the first cap-cell.

Fig. 15. A still more advanced embryo. Vertical median section.

Figs. 17-21. Series of vertical sections through an embryo of five days. Fig. 17, the leaf. Fig. 18, stem. Figs. 19-21, root. In 17 b may be seen the beginning of the vascular bundle of the leaf.

Fig. 21 a. Longitudinal section through the root of an embryo of the same age.

Fig. 22. Series of four transverse sections of an embryo of seven days (not as far advanced as usual). In b and c are seen the indications of the vascular bundles of the root and leaf.

Fig. 23. Median longitudinal section of an embryo of eight days, still surrounded by the prothallium-cells and showing the macrospore. \times about 100.

Fig. 24. The basal part of the same embryo. \times 300. i, intercellular spaces. r, apex of the root. s, apex of the stem.

Fig. 25. Second leaf of the same embryo.

Figs. 26-29. Details of the structure and division of the nuclei of the young embryo. All examined with a $\frac{1}{10}$ oil-immersion lens. Fig. 26 from a two celled embryo. Fig. 27, embryo of four days. Fig. 28, embryo of five days; alcoholsafranin-preparation. Fig. 29, embryo of eight days.

PLATE XV.

Fig. 1. Transverse section through the apex of the stem of an embryo of nine days. a, apical cell of the stem. L^2 , the second leaf. The vascular bundle of the first leaf lies above. \times 300. Alcohol-gentian-violet-preparation.

Figs. 2-5. Series of transverse sections through the root of an embryo of the same age. a, b, sections through the root-cap, the others through the root itself. i, intercellular spaces. Alcohol-Bismarck-brown-preparation. \times 300.

¹ The expressions four days, five days, etc., will be understood to mean from the time the spores were first placed in water.

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Fig. 6. Transverse section near the base of the first leaf of an embryo nine days old. i, intercellular spaces. Alcohol-gentian-violet-preparation. × 300.

Fig. 7. Vertical section of an embryo thirteen days old showing the second root. \mathbb{R}^2 . \times 300.

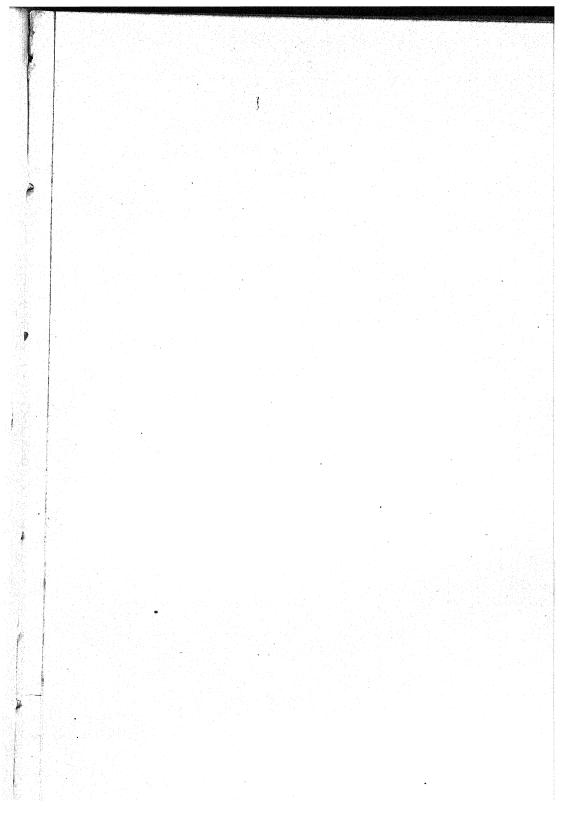
Fig. 8. The second leaf of the same embryo. × 300.

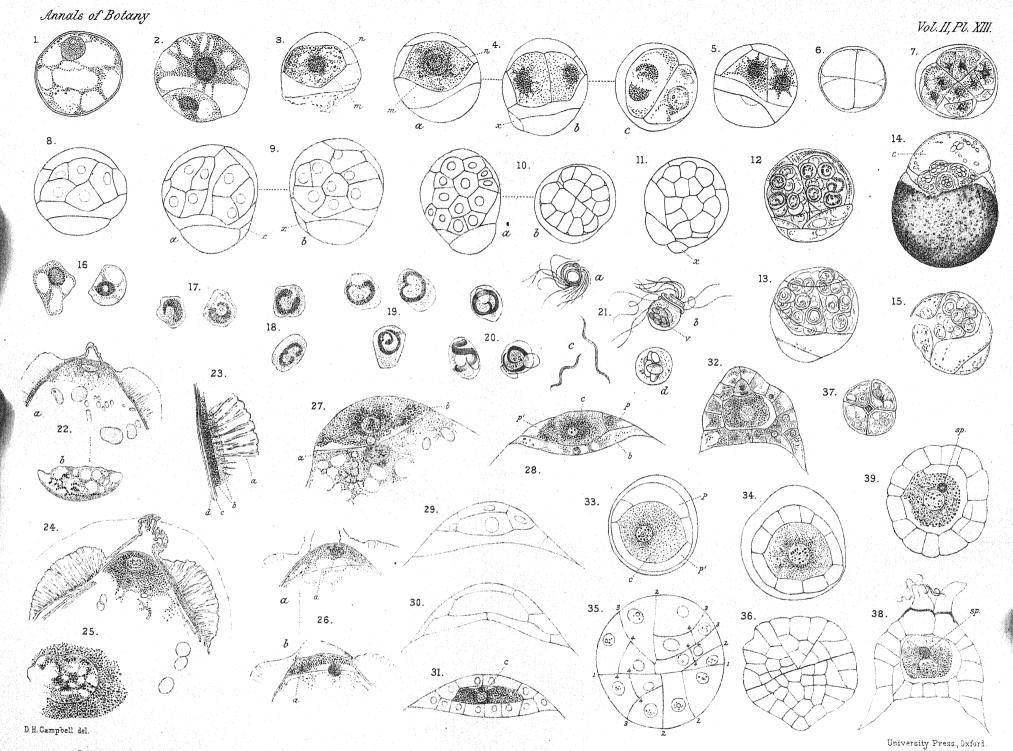
Fig. 9. Longitudinal section through the apex of a young plant that had four fully-developed leaves. s, Apex of the stem. L, L^1 , young leaves. r, a young root. \times about 100.

Fig. 10. Transverse section of a leaf of the same embryo. \times 48.

Fig. 11. Vascular bundle of the same. x 300.

Figs. 12-13. Stomata from the first leaf. \times 300. Fig. 12 in longitudinal optical section Fig. 13 from the surface.

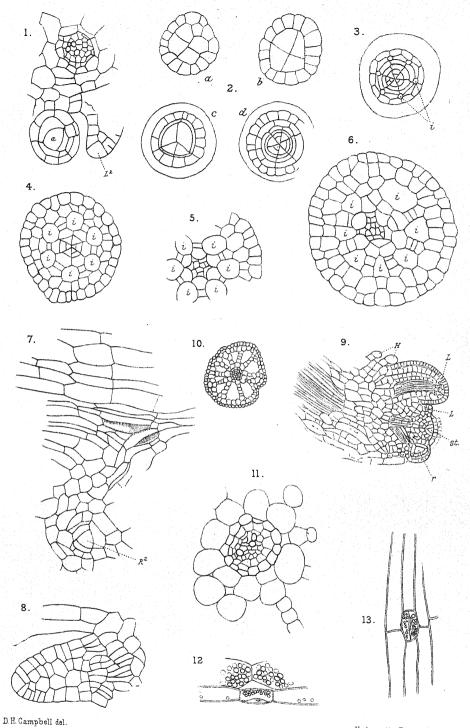




CAMPBELL. - DEVELOPMENT OF PILULARIA GLOBULIFERA.



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A structural and systematic account of the genus Struvea.

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AND

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With Plate XVI.

HE genus Struvea was founded by Sonder in 1845, in a paper in the Botanische Zeitung for that year, in which he described the new algae collected by Preiss in his Australian travels. The name was chosen in honour of H. de Struve, Ambassador from Russia to the Hanseatic Towns, and a patron of Natural History. The only species described was S. plumosa, Sond., subsequently figured by Kützing² and later by Harvey³. In the same volume Harvey figures the next species known under the name S. macrophylla, both forms being remarkable for their graceful habit. We have examined Harvey's specimens of S. plumosa in the British Museum, and Dr. Perceval Wright with great kindness sent us for examination not only the unique of S. macrophylla, known to Harvey at the time of its publication, but also a specimen collected later in the same region (West Australia) by Mr. G. Clifton. Harvey's unique is a bleached specimen, but the later one retains its

[Annals of Botany, Vol. II. No. VII. November 1888.]

¹ Nova Algarum genera et species, quas in itinere ad oras occidentales Novae Hollandiae, collegit L. Preiss. G. Sonder, in Botan. Zeit. 1845, p. 49. ² Tab. Phyc. Bd. vi. pl. 90. ³ Phyc. Austr. vol. i. pl. 32.

green colour. Kützing describes and figures 1 two forms, which he names S. scoparia and S. delicatula. They were both collected by Vieillard in New Caledonia. Dr. Suringar, the happy possessor of the Kützing Herbarium, has been good enough to lend us the type specimen of S. scoparia, and, from an inspection of it, we have no hesitation in excluding it from the genus. It agrees in all respects with the neighbouring genus Apjohnia, and though hardly in perfect accord with A. laete-virens, Harv., we have not sufficient reason to separate it from that form. S. delicatula is no doubt a Struvea, and from a comparison of Harvey's specimens of his Cladophora? anastomosans 2 (published seven years before) there appears to be equally little doubt that it too belongs to the same species. Dr. Grunow has kindly called our attention to certain Ceylon specimens collected by Mr. Ferguson (No. 98), and it is right to add that the examination of a series of these has materially helped us to this conclusion, in which we find we have been anticipated by M. Crouan3. The next form recorded was collected by the 'Challenger Expedition' from thirty-one fathoms off Bermuda, and described by Prof. Dickie 4 under the name of S. ramosa. Since then Drs. Piccone and Grunow have published 5 a form from the Canary Islands to which the name was given of S. anastomosans (Harv.) var. canariensis. Dr. Piccone mentions, in a note, that he intended to make this plant the type of a new genus to be called Cormodiciyon, but he wisely gave way to the eminent Dr. Grunow, who insisted on its being a Struvea. The authors, however, are mistaken in quoting S. anastomosans, Harv., since the Cladophora anastomosans of Harvey, although published previously, is none other than S. delicatula, Kütz. In the second place, Dr. Grunow, never having seen specimens of S. ramosa, Dickie, was thus prevented from placing the

¹ Tab. Phyc. vol. xvi. p. 1, Tab. 2.

² Phyc. Austr. vol. ii. pl. 101.

Mazé et Schramm, Algues de la Guadeloupe.
 Linn. Soc. Journ. Bot., vol. xiv.

⁵ Crociera del Corsaro. Alghe, 1884.

Canary Island form under it as we have now done, after inspecting a specimen kindly sent us by Dr. Grunow. In 1878 Zanardini described 1 a very beautiful minute form collected by Dr. Beccari, in New Guinea, under the name of S. tenuis. We have to thank Dr. Beccari for the opportunity of examining this species.

Passing over for the present the hitherto unpublished form sent us by Dr. Grunow, under the MS. name of S. delicatula, Kütz., var. Caracasana, Grun., we now come to what is perhaps the most striking and beautiful of all forms of Struvea. Dr. J. E. Gray, in his paper on the genera Anadyomene and Microdictyon², established the genus Phyllodictyon to include a very remarkable specimen collected by Mr. Menzies in the Gulf of Mexico in 1802, and preserved in the Herbarium of the British Museum. This very fragile specimen, large as it is (I foot by 3 inches), is but a fragment of the whole plant, as the remains of the stalk clearly show. It was probably about an inch higher and six or seven inches in breadth. (See reduced Fig. 4 a.) Though so much larger than S. macrophylla the texture of the frond is even more delicate.

Dr. Agardh, in his recent monograph of Siphoneae, gives an account of the genus as known to him at p. 108. He merely enumerates the four species and one variety known to him (some of them by name only), and records his doubt as to whether they all belong to the same genus. So many more forms have become known to us, and we have obtained access to so much material, that we venture to hope that the following account may in some degree improve upon the unsatisfactory state in which Dr. Agardh was compelled to leave the genus.

THE STALK consists of a single cell from its earliest stages up to the time of formation of the frond, when a transverse wall is formed a short distance below the base of the frond. The form of the stalk, however, differs greatly according to the species.

¹ Phyceae Papuanae Novae, in Nuovo Giorn. Bot. Ital. x.

² Journ. Bot. 1866, p. 69.



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In S. plumosa (Fig. 1 a) the stalk is at first club-shaped with a smooth and delicate wall in which, as well as in the nature of its contents, it very closely resembles some species of Valonia (Fig. 1 b). At a later stage it becomes annularly corrugated below, while the apex remains smooth and obtuse. In this condition it increases in length, and ultimately the upper part becomes prolonged into a slender corrugated filament, from the apex of which a cell is cut off which, by subdivision, produces a series of ten or twelve cells one above the other, which, by their branching, give rise to the whole of the frond. This statement is derived from Harvey's description 1, which we have been unable to verify as regards the first stages in the formation of the frond, because the specimens of S. plumosa accessible to us do not include any of the exact age required. The mature stalk tapers slightly at both ends, and is corrugated throughout (Fig. 1c). By making a longitudinal section of a well-developed frondless stalk, we came to the same conclusion as Harvey and Agardh, viz. that the cavity of the stalk is not interrupted by any transverse walls. The outer wall is so much thickened, and in the older specimens encrusted with a Melobesia in addition, that without making a section one would probably be unable to detect septa if they were present. The constrictions are only inflexions of the membrane. The wall is formed of a great number of layers, and when cut or otherwise roughly treated the inner layers tend to break up into fibrils, as observed by Agardh 2 in the nearly related genera Apjohnia and Chamaedoris. A similar fibrose structure is described by us in the present volume (p. 171), in a paper on Spongocladia; it is of course connected with the striations seen in surface view in all these cases. The older stalks are incrusted in various degrees with calcareous algae, chiefly a Melobesia, which Harvey refers to as a thin coating of calcareous matter, making it one of the characters of the genus. According to Leitgeb 3 the

Phyc. Austr. pl. 32.
 Quoted from Bot. Zeit, 1888, No. 14; Sitzb. Kais. Akad. d. Wiss. in Wien, Bd. 96.

incrustation of Acetabularia consists chiefly of calcareous algae, just as in the present genus.

We have seen only one branched specimen in *S. plumosa*, in which two stalks sprang from a very short common sac-like base. In *S. macrophylla* (Fig. 2 a) the stalk tapers slightly from the middle towards each end, is corrugated throughout, and resembles that of *S. plumosa*; and it is presumable that the stages of development are the same in the two species, for they seem nearly related to one another.

In S. ramosa the stalk has a very different appearance from that of the two species just mentioned. It is here filiform and of about equal diameter throughout, except for a few transverse corrugations which occur usually at the base of a stalk, but are sometimes absent altogether and would be overlooked at the first glance owing to the small diameter of the stalk. The stalk is often branched in this species, in which case the branches generally show a few corrugations at their bases. Branching is generally opposite, Fig. 3 b being a typical example. The branches here are of about equal value, but in some specimens the central filament branches again. Before the frond is formed the stalk is simply an erect cylindrical unicellular tube. Dickie, after describing S. ramosa, mentions the presence of a 'thin, reddish, calcareous coat at the lower part' of the stipes, as one of his reasons for referring it to the genus Struvea. This calcareous coat is however, as in S. plumosa and S. macrophylla, evidently due to incrusting algae.

In S. pulcherrima (Fig. 4 a) the stalk is filiform, cylindrical, and smooth (where it is visible, being mostly enveloped by a short tufted red sea-weed—no Melobesia being present). It is apparently branched into three filaments, each of which is again divided into four, but as the whole system bears only a single frond, it is better to regard the branches as forming the lower part of the frond. In S. ramosa the stem was regarded as branched, because each of its divisions bore a perfectly distinct frond; but taking a single frond of this species, it is seen that the filament bearing it divides into three branches, which remain simple for a short distance before



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entering, or rather forming, the frond. If these three branches were increased in length below the frond they would produce an arrangement approaching that of *S. pulcherrima*.

S. tenuis has a very minute stalk (Fig. $5\,a$), which bears a greater proportion to the frond as to length than is the case in S. plumosa. It is smooth with a delicate wall, and below the frond there is a septum in the usual position, i.e. at a distance below the frond a little greater than the length of the lowest cell of the midrib. The stalk is unbranched except in one specimen, where it is forked about half way up; one of the branches bears a frond, but the other is simple.

The stalk of *S. delicatula* is never corrugated. It is simple or branched, and usually of about the same diameter as the midrib (Figs. 6a, 7a, 8a).

THE ROOTS of S. plumosa (Fig. 1 a) are given off laterally from the lowest quarter-of-an-inch of the base of the stalk; they are very tenacious, branched, irregularly septate, occasionally transversely corrugated, bearing discs or tufts of root-lets here and there which are sometimes very like the organs of attachment to be described in the frond. The roots contain a great number of starch-grains and sometimes chlorophyll, even in the ends of their branches; they become very much entangled and matted together, so that the stalks, which grow together in tufts, can often only be separated by tearing some of their roots.

It seems very probable that vegetative multiplication may take place by some of the roots assuming the character of creeping rhizomes, which produce vertical frond-bearing branches.

In support of this it may be mentioned that a root of S. plumosa connected with a frond bore a vertical branch which, though small, was very like a young stem. S. macro-phylla has well-developed roots, but they have relatively thin membranes and an almost entire absence of cross walls, but numerous rhizoid attachments. The roots of S. delicatula are generally very septate and irregular (Fig. 8 c). S. ramosa has very slight development of roots in the specimen where the

base of the stem was best seen. In *S. tenuis* they were hidden, and in *S. pulcherrima* they were not very clear owing to the fragments of shell, etc. to which they were attached.

THE FROND of S. plumosa is formed, according to Harvey, by the subdivision of the apical cell into a vertical series of cells, each of which produces from its shoulders two opposite branches, at first free and pectinate, then once and again pinnulate, the pinnulae 'anastomosing' and producing the network. Agardh supposes that an apical cell is repeatedly cut off and a pair of branches formed below it each time. If this be so, and Harvey's Fig. 4 makes it probable, then this species differs in the mode of development of its frond from that of S. tenuis, which is described below.

The filaments composing the frond of *S. plumosa* show striation of their walls very well (Fig. 1 h); it is seen equally well in the young stalk before it becomes too much thickened. Longitudinal and transverse striations are easily observable. The former appear to be more numerous in the outer layers of the cell wall, the transverse ones in the middle layers, and the longitudinal again in the innermost. Fig. 1 h shows these striae in one of the cells of the midrib. In some cases only the longitudinal striations are to be seen. Longitudinal and transverse striae of this kind are mentioned by Thuret 1, and were held by him to be characteristic of the genus *Conferva*, but they have since been described in other genera, as mentioned above, in connection with the stalk.

The structure of the frond of *S. plumosa* is very regular, the primary veins or pinnae being given off in opposite pairs from the midrib at an angle of about 60°; they remain parallel to one another for some distance and then each curves upwards and inwards, attaching itself by its apex to the lower side of the similarly curved pinna next above it.

The frond is regularly crenate, its margin being formed by the curved ends of the pinnae, which produce no branches from their outer side where they form part of the margin.

¹ Annales des Sciences naturelles, Bot. sér. 3, Tome III (1845), p 274.

Thus the tips of the pinnae form exceptions to the rule of opposite branching which prevails elsewhere in the frond of this species, because they give off pinnules on their upper side only (Fig. 1 e). The pinnae are constricted at regular intervals so as to appear to consist of a series of segments about twice as long as broad separated by transverse walls. To prove that the apparent septa were not merely annular thickenings, a filament (allowed to swell up in water) was torn at one of the constrictions, and the cross wall was seen to bulge out under the microscope when the filament was pressed. Below each transverse wall of a pinna two (except at the apex) opposite pinnules are given off, which lean slightly forward and attach themselves to the next pinnae on their respective sides (Fig. 1 e). In the lower part of the frond they become constricted at a varying number of points (dependent on the length) and form transverse walls at the points of constriction. In the upper part of the frond the pinnules give off short unicellular branches below some of their septa, thus increasing the complexity and compactness of the frond. Owing to the comparative shortness of the cells which form the pinnae, the pinnules are inserted pretty close to one another, and as they are directed slightly forwards (i.e. towards the apex of their pinna), they cross one another, so that, when looking at the frond, one sees one series of pinnules at the surface partly covering another series below. The length of the pinnules is about 3-5 times their diameter, their articulations being about 1½ times. They are relatively thick, so that in a mature frond there are hardly any interstices to be seen, on account of their overlapping arrangement. The general arrangement of the pinnules in the specimens we have examined is a little different from that shown by Harvey 1.

The mode of attachment of the pinnae and pinnules has now to be described. When a pinnule has by its growth brought its tip into contact with another part of the frond, it forms at its apex a special organ of attachment which we propose to call a *tenaculum* (Fig. 1 f).

¹ Phyc. Austr., Tab. 32.

The tenaculum consists of a ring of radiating branched rhizoids which surround the disc of contact between the apex and the wall of the pinna. The mode of formation of this seems to be that the tip of the pinnule becomes somewhat flattened on the wall of the pinna, and then, from the outermost region of contact, puts out a number of small radiating rootlets which creep along the surface of the pinna, and branch so as to form a compact rosette-like structure, which adheres to the surface of the filament and fixes the pinnule in position.

Careful focussing has led us to believe that these rootlets are entirely superficial, never penetrating the cell-wall, but adhering to it probably by some process like that by which the root-hairs of higher plants adhere to particles of soil.

These organs appear to be formed only in response to contact, like the adhesive discs of *Ampelopsis*, and they are nearly universally terminal in position, only a single lateral tenaculum was seen among all the species. A transverse wall is nearly always formed in the pinnule at a short distance from the apex, thus cutting off a sub-globular terminal cell which bears the ring of rootlets (Fig. 1 f). This wall is evidently connected with the formation of the rootlets, for it seems to be formed only when attachment takes place. A possible function of this septum is to prevent too great loss of contents in case of injury to the delicate rootlets. Fig. 3 e shows a filament of S. ramosa bearing two of these organs at its apex; one or two similar cases were seen in S. plumosa.

As occurring in Valonia fastigiata, Harv., Agardh¹ mentions certain structures, which he terms fibulae. These seem from his description to have the same function as the organs which we have described under the name of tenacula, in our opinion a more appropriate word. His figure (Tab. I, Fig. 5) of these organs shows that they differ a good deal in appearance from those of Struvea, in being lateral and in the different character of the rootlets (if one can so call them), though they

¹ loc. cit. p. 94.

serve the same purpose of attaching branches to one another. Agardh refers to the well-known similar structures in several of the encrusted Siphoneae (Udotea, etc.), though he believes that among these latter their function may sometimes be that of attachment, and may sometimes be connected with the deposition of lime. We examined a piece of Microdictyon Velleyanum, to see if similar organs were present in that genus, and found that an apex of a filament, when it comes into contact with another filament, forms crenations round the edge of contact, which are sometimes sufficiently pronounced to be termed rhizoids, but the attachment, which is very firm, must be chiefly due to cohesion between the filament-surfaces, which is here sufficient without increase of contact-surface by formation of long rootlets like those of Struvea. Tenacula occur also in Spongocladia, where they resemble those of Struvea.

In describing species of Struvea, Harvey¹ and Dickie² both speak of 'anastomosis' of filaments, and Harvey further mentions it among the generic characters. This word cannot be correctly applied to the frond of Struvea, for though the filaments become attached to one another by means of tenacula, there is no resorption of the double membrane which separates the cavities of the cohering filaments. The attachment, however, is sometimes very firm, as in S. delicatula, described

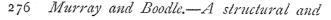
The frond of S. macrophylla (Fig. 2 a) bears a slight general resemblance to that of S. phimosa, but differs in the mode of branching of the filaments which compose it and in its much greater size. The two specimens of this species differ somewhat from one another in detail. The branching and arrangement of the filaments is almost precisely similar, but the frond of the one 3 is oblong-oval, cordate, and strongly crenate, while the other (Fig. 2 a) is oblong-elliptical with a very slightly crenate margin. The midrib is very distinct, and of about the same diameter as the upper part of the stalk. The primary branches or pinnae are given off oppositely from the midrib

¹ Phyc. Aus., Pl. 7 and 32. ² Linn. Soc. Journ. Bot. vol. xiv. ³ Harv. Pl. 7.

at angles varying, from below upwards, from 90° to about 45°. The secondary branches are very regular and so arranged as to produce zigzags connecting each pair of primary branches. The tertiary branches run parallel to the primary, three or four bridging over the V-shaped space between two pinnules, and enclosing elongated meshes.

Quaternary branches are formed here and there. The frond of the bleached specimen, which Harvey described, is a good deal incrusted with calcareous algae, but this may have taken place after the death of the plant.

In S. ramosa the frond has a midrib and pinnae, which are rather inconspicuous as their diameters are not much greater than that of the pinnules (Figs. 3 α and 3 c). The lowest cell of the midrib and the lowest cell of each of the two basal branches are elongated in the mature (?) frond. The branching in some of the specimens is very regular. Two or four branches are given off from the top of each cell of the midrib, and their pinnules become attached to one another and to the pinnae and midrib, so as to form a reticulum which has usually triangular meshes (Fig. 3c). The margin of the frond generally has projecting pinnae and pinnules, which probably shows that the specimens are not mature. The regularity of the reticulum varies very much in the different specimens, and sometimes in different parts of the same specimen. Similar irregularity is seen in S. delicatula and in S. tenuis, where it is sometimes due to injuries, but at other times merely to change in the angle of branching or suppression of some of the branches, where no injury is apparent. Branching in S. ramosa often takes place before the formation of a transverse wall, as shown in Fig. 3 f, but that septa are ultimately formed was proved by examining the ends of filaments which had been torn up, as was done in S. plumosa. The tenacula are here very much like those of S. plumosa, but, like the whole of the frond, they have thinner walls than the latter species. The rhizoids are well developed, and very delicate (Fig. (3 d). By focussing the cell-wall at the apex of the tenaculum, three or four pits with granular contents are often seen. They



must be the mouths of tubes which, by their repeated branching, produce the whole of the rootlets.

In addition to these usual organs of attachment, there are also remarkable structures of the kind at the bases of some of the filaments of the frond, which in shape resemble the sporangia of Botrydium (Fig. 3 h). They have evidently been produced by the formation of a small wart-like outgrowth from the base of a branch just above its basal wall. The outgrowth then grew downwards parallel to the filament, producing a neck-like prolongation which curved inwards and came into contact with the surface of the filament below the transverse wall, and then threw out a fan-shaped mass of branched rootlets on the wall. These organs occur in the specimen examined at the point of origin of the frond, where the stalk divides into three filaments, each of which has two of these organs at its base (Fig. 3g); there are three or four at each of the next two points of branching of the midrib, and, at a point in the stalk where there is a transverse wall, five or six of these clamps connect the part of the stalk above the cross-wall with that below.

Similar bodies were detected at the base of the frond of Dr. Piccone's specimen, but nothing like them has been seen in the other species of *Struvea*. From the arrangement of contents these bodies do not seem to be cut off from the cavity of the filament which produces them.

The frond of *S. pulcherrima*, as stated above, is supported by three main filaments. Its outline and dimensions cannot be determined, owing to the fragmentary nature of the specimen, but the probable shape is that given in Fig. 4 α , and the size would be about 10 inches in length by 6 to 7 inches in breadth. Each of the three filaments branches into four; these remain simple for a short distance and pass into the frond, where they are traceable as veins, which in their turn produce veinlets, and the branching is repeated several times, so that, by the attachment of the ultimate branches to each other and to the veins, a very perfect network is formed (Fig. 4 b). The veins and veinlets generally give off two or four branches just below their transverse walls, but here and there

an arrangement occurs which reminds one of the branching of the main filaments in *Anadyomene*. One of the cells is club-shaped, and from its swollen end gives off five or seven branches of about equal value, though smaller than itself, and separated from one another by nearly equal angles.

The frond appears septate throughout; a small piece was tried, as in S. plumosa, and found to have real transverse walls.

The tenacula have very well-developed rhizoids, and adhere very closely to the filaments.

S. tenuis (Fig. 5 a) has a shortly ovate cordate frond with 5-7 pairs of pinnae, which form a crenate margin by their incurved apices, and give off pairs of pinnules, mostly united with one another in a very regular manner, the apex of one attaching itself to the middle of another (see Fig. 5 b). Transverse walls appear to be formed rather late: thus in Fig. 5 c there are only one or two present, the other transverse marks being slight constrictions.

The very regular arrangement seen in Fig. 5 b does not seem to be constant in this species, for in another specimen the mode of attachment varies in different parts of the frond; one pinnule gives off two branches, and some of the pinnules attach themselves to the pinnae instead of to each other. A very early stage in the formation of the frond is seen in Fig. 5 d, which shows five pairs of protrusions below the apex, and below them a constriction, which will probably be the point of formation of the septum in the stalk below the frond. Although slight creases are seen in one or two places, we think there is no doubt that the whole is a single cell. This agrees with the late formation of the transverse walls in the pinnae. In S. plumosa the pinnae form their transverse walls before giving rise to pinnules, so it is very likely that in the formation of the frond cell-walls would precede the branch protusions, in that species, as described by Harvey.

S. delicatula (Fig. 6 a) is the most variable species of the genus. On comparing Kützing's figure of this species with Harvey's figure of his Cladophora? anastomosans one would not be much disposed to unite the two, but in looking through



278 Murray and Boodle.—A structural and

a large number of the specimens of this species collected by Ferguson, we found that the fronds exhibited almost every degree of reticulate cohesion between the two types, and equally wide variations in the angle of branching, size of ultimate branches, etc., so that it is hardly possible to make a diagnosis to suit all the specimens.

The branching in the frond of most of Harvey's specimens is rectangular, and the reticulum very perfect; this is also the case in several of Ferguson's specimens (Fig. 6 b), but in many of the latter the cohesion of branches is very imperfect, whole pinnae with their pinnules remaining free from one another or united only at one or two points. The cohesion evidently begins at different times in different individuals, for in some the fronds show a reticulate structure when they are still very small, but in others the pinnae grow to a considerable length before the pinnules become attached, thus producing a frond like that in Kützing's figure; but we are of opinion that these forms would, when older, become like the more reticulate forms. The angle of branching is sometimes acute, but when the pinnae have become united with one another by means of their pinnules, if, as is probable, growth ceases in the pinnae in acropetal order, they become straightened out so as to stand at right angles to the midrib. The lower parts of the frond are often, as in S. macrophylla, more rectangular than the upper.

The specimens of S. delicatula, var. Caracasana (Fig. 7 a), have regularly bipinnate fronds, and the pinnules have only become attached in one or two places (Fig. 7 b), but, from the mode of attachment, the fronds must be pretty nearly mature.

One very anomalous form (Fig. 8 a) was collected by Ferguson; it has very upright branches, and we should have classed it as an oppositely branched *Cladophora*, but for the following facts:—the character of its roots and stalk is exactly the same as that of the specimens of the *Struvea delicatula*, with which it is associated, its plan of branching (although more upright) is very much the same, and here and there the

branches are united by terminal organs of attachment precisely the same as the tenacula of S. delicatula. The branching takes place oppositely, and in one plane, but as the branches are mostly free they become more or less irregularly arranged when dried (Fig. 8 b).

S. delicatula often grows in tufts with the fronds attached to one another by some of the pinnules of one adhering to the other frond by their tenacula. In one of the erect forms the end of a branch has attached itself by a tenaculum to a small piece of shell, which had fallen on the top of the tuft.

The attachment of the branchlets must be very firm, because, when two pinnules are torn apart, the tenaculum of the one sometimes tears off the outer layers of the wall of the other. Prolification of filaments sometimes occurs in *S. delicatula*, as seen in Fig. 6 d, where the old filament must have broken off and a transverse wall helped in the formation of a new filament.

We have been unable to find any traces of reproductive organs in any of the species of *Struvea*. In *S. plumosa* Kützing observed in one of the filaments ¹ some dark green granular spherical bodies which he calls 'Keimzellen (?).' They may be reproductive bodies, of some kind, but they remind one of the often spherical masses into which the protoplasm and chlorophyll of a cell of *Cladophora* frequently resolve themselves when the wall has been injured and the turgidity destroyed.

Until the reproduction of *Struvea* has been discovered its systematic position must remain doubtful. It is indissolubly linked with *Chamaedoris* and *Apjohnia*, and the evidence before us seems to point to this group as occupying a position among Siphoneae (sensu Agardh) near to *Valonia*, but connecting this series of forms with other green algae, such as *Cladophora* and *Spongocladia*.

¹ Tab. Phyc., Bd. vi. Tab. 90 f.

DISPOSITIO SYSTEMATICA.

STRUVEA Sond. Bot. Zeit. (1845), p. 49.

Alga viridis, marina, erecta, stipitata, flabelliformis. Stipes simplex vel ramosus, radicatus, monosiphonius, continuus, in aetate majore reticulo flabelliformi, costato, coronatus. Reticulum ex filis confervoideis plus minusve articulatis, pinnatis, apice per tenacula radicantibus, evolutum.

Syn. Phyllodictyon, J. E. Gray, Journ. Bot. (1866), p. 69. Pterodictyon, J. E. Gray, loc. cit., p. 70. Cormodictyon, Piccone in Crociera del Corsaro (1884), p. 21.

1. Str. plumosa¹, Sond., loc. cit., p. 50. Stipes rugosus, reticulo oblongo-ovali (1-2 uncias longo) crenato, coronatus; filis 2-3-pinnatis; articulis pinnarum diametro 2-3-plo, pinnularum sesqui-longioribus. Harv. Phyc. Austr., Tab. xxxii. Kütz. Tab. Phyc., Bd. vi. Tab. 90.

Hab. ad oras occidentales Novae Hollandiae legit Preiss, Harvey! Clifton.

2. Str. macrophylla, Harv. Phyc. Austr., Tab. vii. Stipes rugosus, reticulo oblongo-ovali grande, spectabili (4-6 uncias longo, 2½ uncias lato) crenato, coronatus; filis pluries pinnatis, articulis pinnarum 5-6-plo, pinnularum 3-4-plo, diametro longioribus.

Hab. ad oras occidentales Novae Hollandiae legit Mrs. Drummond! Clifton!

3. Str. ramosa, Dickie, in Linn. Soc. Journ. Bot., vol. xiv, p. 316. Stipes rugosus, sursum opposite ramosus, reticulis subellipticis; filis tripinnatis, articulis inferioribus pinnarum 7–8–plo, superioribus 3–4–plo, diametro longioribus.

Syn. Struvea anastomosans, Harv. (sic.) var. canariensis, Picc. et Grun. in Crociera del Corsaro, Genova (1884), p. 20.

Hab. ad Bermudam, ex profundis extracta. H.M.S. 'Challenger'! et ad insulas Canarienses legit Piccone!

¹ We have seen, in the Edinburgh Herbarium, a type specimen of *S. plumosa* collected by Sonder. The plants, though younger, have very much longer stalks than Harvey's, and an examination of the young frond confirms the view expressed above as to its development.

4. Str. pulcherrima, nob. n. sp. Stipes laevis reticulo oblongo, cordato, tricostato, maximo (10 uncias longo, 6–7 uncias lato) coronatus; filis iterum atque iterum pinnatis, articulis pinnarum diametro 3–4–plo, pinnularum 2–plo longioribus.

Syn. Phyllodictyon pulcherrimum, J. E. Gray, Journ. Bot.

(1886), p. 70.

Hab. in sinu Mexicano legit cl. Archibald Menzies 1!

5. Str. tenuis, Zanard. in Nuovo Giorn. Bot. Ital. (1878), p. 39. Stipes laevis pusillus reticulo pulcherrimo, cordato-ovato, tenuissimo (½ unc. et longo et lato) coronatus; filis bipinnatis articulis diametro 2–3-plo longioribus.

Hab. ad Sorong, Nova Guinea legit O. Beccari!

6. Str. delicatula, Kütz. Tab. Phyc., Bd. xvi, Tab. 2. Stipes laevis, simplex vel ramosus, pusillus, reticulo subpyramidato (1–2 uncias longo), coronatus; filis distiche pluries pinnatis, pinnis pinnulisque oppositis horizontaliter patentibus, hic illic applicatis.

Species quam maxime variabilis.

Syn. Cladophora? anastomosans, Harv. Phyc. Austr., Tab. ci. Hab. ad Novam Caledoniam leg. Viellard; ad oras occidentales Novae Hollandiae leg. Harvey! ad Ceylonam leg. Ferguson! ad ins. Guadeloupe leg. Mazé!

Var. Caracasana, Grunow, in lit. filis reticuli regulariter bi-

pinnatis.

Hab. ad Cap. Blanco Caracas leg. Gollma!

Species exclusa.

Str. scoparia, Kütz. Tab. Phyc. Bd. xvi, Tab. 2=Apjohnia laete-virens, Harv.

Cl. Grunow misit sub nomine *Valoniae radicantis*, Grun. (Adelaide, Nova Hollandia) et *Valoniae rhizophorae*, Grun. et Picc. (Suakin in mari rubro) duas species immaturas forsan *Struveae*.

¹ On searching Menzies' own Herbarium in Edinburgh Botanic Garden we found another specimen of *S. pulcherrima*—unfortunately even more incomplete than the one referred to. It however exhibits perfectly the beautiful structure of the frond, and bears the additional information that it was dredged from 20 fathoms.

EXPLANATION OF FIGURES IN PLATE XVI.

Illustrating Messrs. Murray and Boodle's paper on the genus Struvea.

Fig. 1. a, Struwea plumosa (nat. size). b, c, d, Stages in development of S. plumosa (nat. size). e, Part of nearly mature frond $(\times 6)$. f, Apex of filament with tenaculum $(\times 60)$. g, Melobesia coating of part of stalk $(\times 5)$. h, Striations of membrane of midrib (highly magnified).

Fig. 2. a, S. macrophylla (nat. size). b, Part of frond of S. macrophylla (× 2).

Fig. 3. a, S. ramosa, unbranched specimen (nat. size). b. Branched specimen showing rugae (nat. size). c, Part of frond of S. ramosa (× 6). d, Tip of filament with tenaculum; the rootlets are seen partly in surface view (× 130). e, Pinnule bearing two tenacula (× 30). f, Pinnule forming two branches (× 30). g, Base of frond showing position of clamps (× 30). h, One of the clamps more highly magnified (× 130).

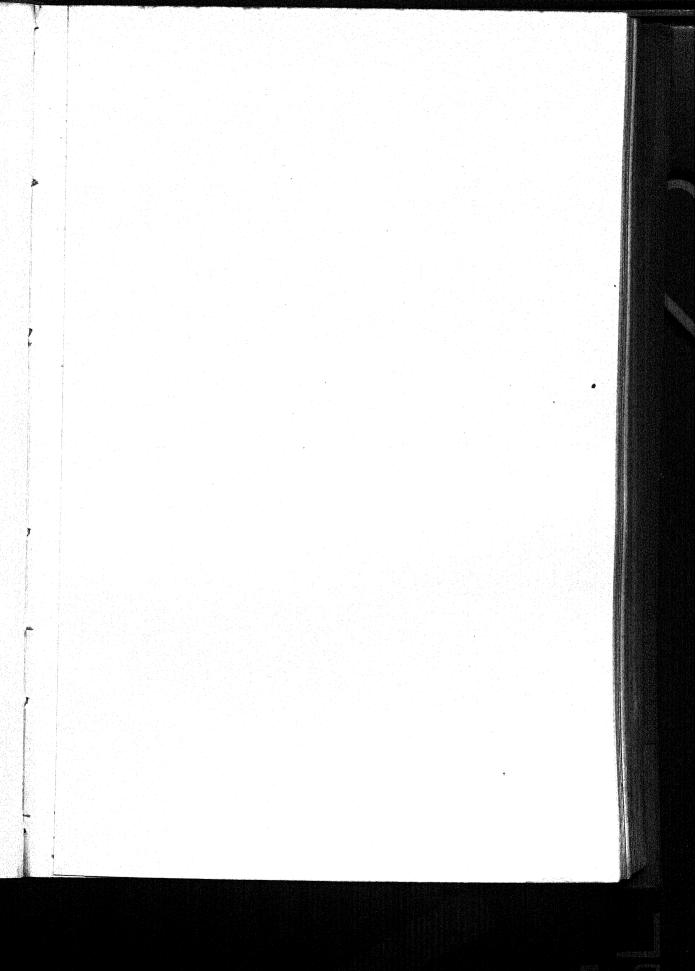
Fig. 4. a, S. pulcherrima restored and reduced to one fourth. b, Part of frond $(\times 6)$.

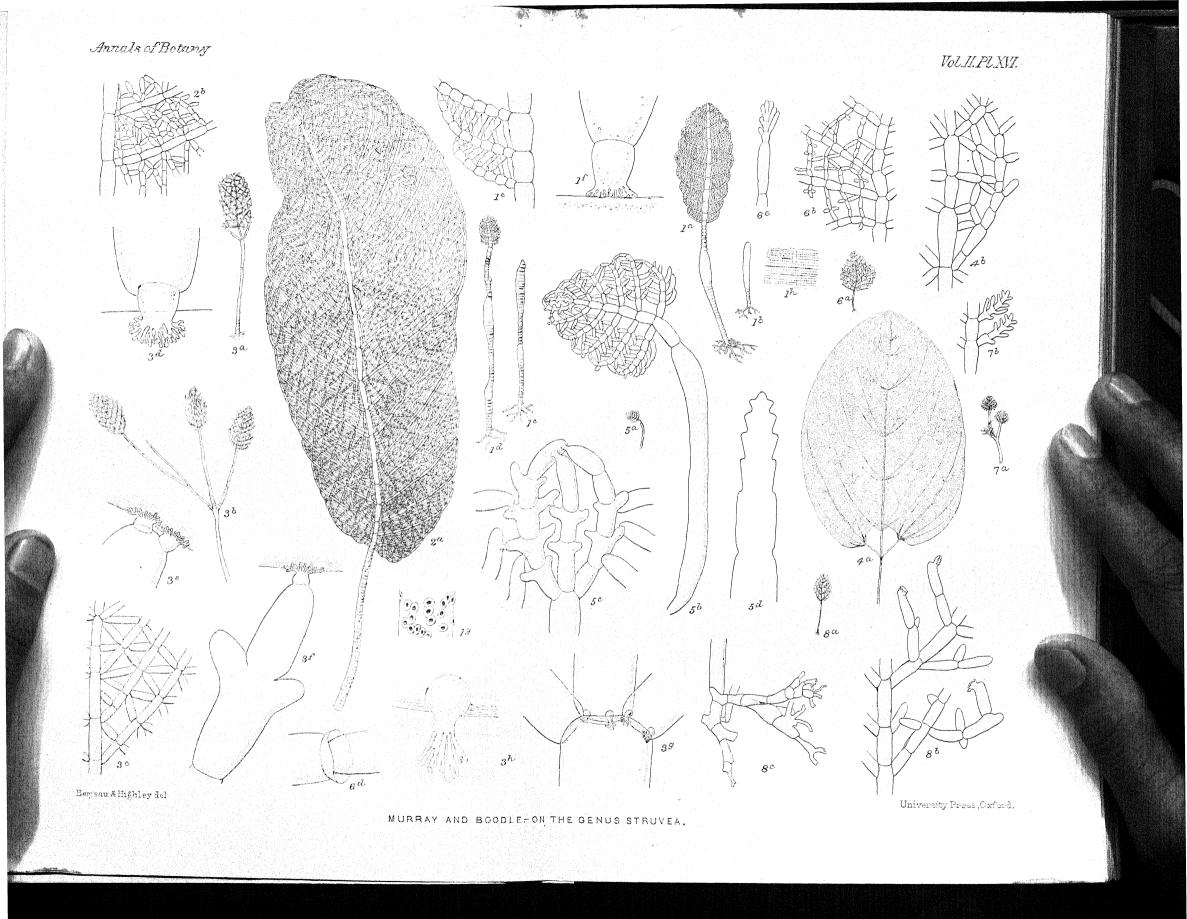
Fig. 5. a, S. tenuis (nat. size). b, The same magnified (\times 10). ℓ , Upper part of frond (\times 40). d, First stage in formation of the frond (\times 35).

Fig. 6. a, S. delicatula (nat. size). b, Part of frond $(\times 6)$. c, Early stage in formation of frond $(\times 6)$. d, Case of prolification $(\times 30)$.

Fig. 7. a, S. delicatula var. Caracasana (nat. size). b, Part of frond (x 6).

Fig. 8. α , S. delicatula erect form (nat. size). b, Part of frond (\times 36). c, Roots of same (\times 30).





DEPARTMENT OF BOTANY, UNIVERSITY OF ALLAHABAD,

Contributions to the Morphology of the Mistletoe (Viscum album, L.).

BY

SELMAR SCHÖNLAND, Ph.D.

With Plate XVII.

DURING the past few years I have repeatedly had opportunities of observing a large number of abnormalities in the structure and arrangement of the organs of the mistletoe, many of which have been noticed before, while others are apparently new. They have led me to give interpretations to some morphological characters of this plant different from those hitherto given, and I therefore think they are worth describing.

In the present paper I propose to deal chiefly with the morphology of the flowering shoots, including both the arrangement and the general structure of the flowers. In order to make my remarks more intelligible, I have included almost all that has been said on the subject by Wydler 1 and Eichler 2.

The mistletoe is dioecious 3 . The plants of the two sexes have on the whole the same structure. The axis of the seed-ling produces two cotyledons and a pair of foliage-leaves alternating with these. It then ceases to grow any further, but in the axils of the foliage-leaves buds are produced which develop into branches the next year. Each branch bears at its base two minute opposite scale-leaves, the prophylls of the new shoot (p, p) in the diagrams); they are at right angles to the bract of the shoot (B in the diagrams). Near the top of

¹ Flora, 1860, p. 443.

² Blüthendiagramme, ii. p. 552.

³ Only a single case in which a male plant had also produced some female flowers and fruits is mentioned by Masters in his Vegetable Teratology, p. 509. [Annals of Botany, Vol. II. No. VII, November 1888.]

a branch two foliage-leaves (L, L, Figs. 1, 2, etc.) are usually found, which alternate with the prophylls, and are therefore median. During the first years the apex of each shoot is either naked, or it bears two more scale-leaves, which again alternate with the foliage-leaves, but the growth is always continued by buds springing from the axils of the latter, and thus the well-known pseudo-dichotomous structure of the mistletoe is produced. The foliage-leaves normally last only one season, while the prophylls may remain for a period of eight or more years. In about the fourth or fifth year of the life of the plant a small capitate inflorescence is produced at the top of each shoot.

It commonly happens that foliage-leaves or shoots are not developed in places where the general plan of the plant would lead us to expect them. The shoots especially may remain dormant for several years. If only one shoot is developed, it often appears as the direct prolongation of its mother axis. If this goes on for several years a sympodium is produced which is frequently of considerable length. It also happens sometimes that new shoots are produced in the axils of the prophylls, and thus false whorls of three to six shoots are formed. As this may be repeated in the case of the accessory shoots, their number may be increased still more, and Wydler 1 found as many as twelve in one case; he also saw prophylls developed into foliage-leaves. Shoots bearing a whorl of three foliage-leaves are not rare, whereas whorls of four foliage-leaves2 are uncommon, but I found them in both male and female plants. The increase in the number of foliage-leaves seems on the whole to be more frequent in the male plants. As a rule, this is due to the substitution of a trimerous or tetramerous whorl for the normal dimerous whorl, as is shown by the fact that each of them may

¹ Flora, 1860, p. 445.

² In one case I found five foliage-leaves in a rather irregular whorl. This was due to the fasciation of two shoots, one bearing two, the other three leaves. The true nature of this abnormality was clearly shown by the internode being groved, etc., also by the structure of the two inflorescences which terminated this double shoot.

bear an axillary bud, and thus true whorls of three or four branches may also be produced. I have actually observed such true whorls of three and four branches. The structure of the inflorescence, moreover, corresponds usually to the number of foliage-leaves, as we shall see later. In one case only, where three foliage-leaves occurred, they seemed to have arisen from the normal two leaves. One of the three leaves was rather broad, and showed beginning of splitting at the apex, while two others were about the normal size; but neither one nor the other of these had, like the third, a bud in its axil, there was however, a bud between them, which served, as it were, as a common axillary bud for the two together (Fig. 3). It is probable therefore, that they owed their origin to the splitting of one of the normal leaves. The odd leaf of the true trimerous whorls of foliage-leaves is always turned towards the axis (Figs. 4, 5 I), whereas the leaves of the tetramerous whorls are placed diagonally (Fig. 5 II, 6).

The inflorescences are usually found between the two foliageleaves, and normally consist of two lateral flowers at right angles to these leaves, and a terminal flower. Each of the former stands in the axil of a small scale-leaf, the two together thus forming a third whorl of leaves (s, s, Figs. 1, 2). No more leaves are borne directly by the primary axis of each shoot in the male plants, but in the female plants the terminal flower is usually preceded by a fourth pair of leaves, which is like the one preceding it, and continues the regular decussate arrangement of leaves (s1, s1, Fig. 1). Where three or four foliage-leaves are borne by a shoot, the number of the upper scale-leaves is increased at the same rate; this is often also the case with the lateral flowers, but frequently their full number is not developed (Figs. 5 I and 5 II). Very often scale-leaves are only developed where foliage-leaves ought to be, either in the place of one or of both of a pair. This occurs chiefly in shoots which have been dormant one or more years. Very commonly these additional scale-leaves also bear flowers in their axils.

¹ From a remark made by Wydler, Flora, 1860, p. 443, I conclude they may also bear flowers in their axils.

and thus we get an inflorescence of five flowers, as represented in Fig. 7. Such an inflorescence has usually a short stalk, and is like the ordinary shoots provided with two prophylls at the base. Whole inflorescences or single flowers may also be formed in the axils of the prophylls of ordinary shoots.

The terminal flower of the male inflorescence is, as a rule, not preceded by scale-leaves, as indicated above. But Hofmeister 1 has stated that they are present here, as in the female inflorescences. This is really often the case, although not observed by Eichler, but still the structure of the inflorescences in which it occurs is not the same as that of the female inflorescences. I only observed this apparent abnormality in inflorescences developed from dormant buds. I have represented it in Fig. 8 I. It is shown there that in the abnormal cases the shoots of male plants have only three pairs of decussate leaves, as in the normal cases. The abnormality is at once understood by comparing it with a case such as is represented in Fig. 7, and which I have explained already. If in such a case the two lateral flowers are not developed, as frequently happens, a three-flowered inflorescence is produced which, it is true, agrees in its general structure with the normal female inflorescences, but there is one difference (quite apart from the number of leaves) by means of which its true nature may be at once detected. A normal female inflorescence is always transverse (Fig. 1), whereas these inflorescences are always median, which must be the case, as two out of the three flowers composing it are seated in the axils of the equivalents (l, l) of the two foliage-leaves, which are always median. The uppermost pair of leaves preceding the terminal flowers (s, s) in such cases is therefore not equivalent to the uppermost sterile pair of leaves (s1, s1, Fig. 1) in the female inflorescence. If, again, both the lateral flowers and their bracts are suppressed (Fig. 8 II), the resulting inflorescence is exactly like the normal male inflorescence, differing only in its relative position to the mother-axis and the bract of the shoot.

¹ Neue Beiträge, i. p. 553. I am quoting here from Eichler, Blüthendiagramme, p. 553.

In the female flowers the perianth consists usually of two dimerous alternating whorls of scale-leaves, which cohere, more or less, at the base. Their position will be readily understood by a glance at Fig. 1, which has been copied from Eichler². The two carpels which compose the ovary continue the regular alternation. No exception has come under my observation with regard to the number of parts composing the lateral flowers, whereas in the terminal flowers of shoots bearing three foliage-leaves only one whorl of perianth-leaves, alternating with the three scale-leaves which precede the flowers, was observed (Fig. 4). Wydler mentions a case in which a female terminal flower, preceded by two scale-leaves, had also a trimerous perianth. An increase in the number of perianthleaves beyond four has also been described by the same author, and is very likely to be explained in the same way as a similar increase of the organs composing the male flowers, which will be treated of later. Whether any variation in the number of carpels takes place I am unable to say.

The male flowers are, on the whole, built on the same plan as the female ones, but every trace of an ovary is absent in their centre. Each perianth-leaf bears six to twenty pollen-sacs. Hofmeister³ and van Tieghem⁴ consider each of these structures (taken as a whole) as a single leaf. The former bases his view on the development, which shows that it arises apparently as one organ; while the latter bases his view chiefly on anatomical grounds, but he is careful to call them simply polliniferous sepals ('sépales pollinifères'); he does not call them stamens, as one would expect. Eichler, on the other hand, who based his view on a comparison between the structure of the flower of the mistletoe and that of nearly allied forms, came to the conclusion that each consists of two parts, namely of

¹ I have never seen the so-called 'calyculus' of the flowers. It is frequently mentioned that it does not occur regularly, and it seems to be certain that it is only an outgrowth of the axis without leafy character. Compare Hofmeister in Flora, 1854, p. 644 (note); Wydler, in Flora, 1860, p. 445; Eichler, Blüthendiagramme, p. 553.

l. c., Fig. 236, B.
 Ann. d. Sc. Nat. série 5, Tome xii. p. 101.

³ 1. c., p. 539.

a perianth-leaf and an anther. I am inclined to think that his view is right, although I cannot offer much additional evidence to support it. But I may mention that I have often seen the posterior perianth-leaf of lateral flowers forming a compact body with the adjoining perianth-leaf of the terminal flower, both of them bearing their pollen-sacs in their proper places. Now, when we thus see that leaves of different flowers frequently coalesce to form a single structure, we are certainly justified from a morphological point of view to assume that such a coalescence may constantly take place in the leaves of the same flower, if there are other reasons to support such an assumption. Eichler adduces as an argument in support of his view the fact that in other species of Viscum, as also in the nearly allied genera Eremolepis, Phoradendron, and others, the two leaves, which are only hypothetical in our species, may actually become nearly separate; and, further, that it also happens exceptionally in these genera that the flowers possess three perianth-leaves and two anthers, one of the latter being then placed between two of the former, 'certainly the best evidence against Hofmeister's view 1.'

Eichler says that the male lateral flowers are 'always' tetramerous, but I found them frequently to be trimerous or even pentamerous. In the trimerous flowers there was apparently a single whorl of perianth-leaves² substituted for the normal two dimerous whorls, whereas in the pentamerous flowers evidently a splitting of a perianth-leaf with the adnate stamen had taken place (compare the diagrams of the lateral flowers in Fig. 6). The terminal flowers of shoots with a dimerous (and I may add also those with a tetramerous) whorl

¹ See also Schumann in Pringsheim's Jahrbücher, 1887, Bd. xviii. p. 133, where questions of this kind are treated of in a more general way; the case of *Viscum* is mentioned on p. 170. My paper was in the hands of the editors before No. VI. of the Annals of Botany was published. I have noticed with satisfaction that Mr. T. Johnson in his paper in that number, on 'Arceuthobium Oxycedri,' brings forward very strong arguments in support of Eichler's view (cf. Annals of Botany, Vol. II. No. VI. pp. 155 and 156).

² For shortness' sake I am only speaking of perianth-leaves here and in the following passages. It will be understood that I always mean the structures composed of a perianth-leaf and an anther.

of foliage-leaves are usually tetramerous, the outer whorl of perianth-leaves being median, and, therefore, differing in this respect from the terminal female flowers, as will be seen when Fig. 1 and Fig. 2 are compared. It will also be seen that the outer whorl of perianth-leaves of the male flowers has the same relative position as the uppermost pair of scale-leaves in the female ones. The terminal male flowers of shoots with three foliage-leaves usually possess two trimerous whorls of perianth-leaves, the outer one having also the relative position of the three scale-leaves in the corresponding female flowers. Eichler is of opinion that in the common male terminal flowers the two scale-leaves which precede the female flowers are made use of ('werden einbezogen'1) in the formation of the perianth. Although at first sight this appears obvious, I cannot agree with such an interpretation. First of all it may be argued, from a general point of view, that the outer and first formed perianth-leaves take a median position, simply because there is room for them to develop in this position on account of the scale-leaves being absent. If we adopt Eichler's view we must further admit that the male terminal flower is constantly without the inner dimerous whorl of perianth-leaves which the corresponding female flower always possesses. But there is, thirdly, one reason which directly compels us to give up the view brought forward by Eichler. I have already mentioned that dormant buds often produce inflorescences composed of a various number of flowers. I have described the three cases which are the most frequent. Let us compare the two cases represented in Fig. 8 I and II. These two inflorescences were found side by side. It will be admitted that in these two cases the terminal flowers are absolutely equivalent, and yet, if we examine the relative position of their parts, we notice the actual difference which exists between the normal male and female terminal flowers. If, as in Fig. 8 I, the terminal flower is preceded by two sterile scale-leaves, the outer whorl of perianth-leaves is median, and thus alternates with them; but if it is not preceded by them,

¹ It must be said that the German expression is rather vague.

as in Fig. 8 II, this whorl is placed transversely, assuming the position of the scale-leaves which are wanting. I have tested this fact in many cases, and always with the same result. I am thus led to believe that the difference between the terminal male and female flowers, with regard to the position of their parts, is simply caused by the complete suppression in the former of the uppermost (fourth) pair of leaves.

An increase in the number of parts composing the male terminal flowers is not rare. Eichler only knew of pentamerous and hexamerous flowers besides the normal ones; but I have also observed one heptamerous and one decamerous flower1. Eichler explained the abnormal cases known to him by assuming that in the hexamerous flowers the inner dimerous whorl of normal flowers was replaced by a whorl of four members, and in the pentamerous flowers by a whorl of three; but his own figure, which I have copied (Fig. 9), suggests at once the idea that the increase is simply due to the splitting of the two normal members composing the inner whorl2. I have already adopted such an explanation in the case of the pentamerous lateral flowers, where I usually found it to agree extremely well with the position of the parts of the flowers. In the terminal flowers a regular arrangement of the parts cannot always be recognised when their number has been increased, but it is easy to find all intermediate stages between perianth-leaves only slightly divided at the top, and others which are divided down to the base. My explanation covers also the cases in which seven and ten perianth-leaves were found, whereas those adopting Eichler's view would find difficulty in explaining them. The view that the increase is due to splitting may perhaps be strengthened still more when I restate the fact, which I hope has been distinctly proved, that splitting of foliage-leaves also occurs in the mistletoe.

¹ The hexamerous flowers of shoots with three foliage-leaves were also apparently unknown to him, but these must be left out of account here, as in a certain sense they have to be considered as normal.

² I may here call attention to the similarity between our case and the interpretation of the androecium of Cruciferae, regarding which Eichler holds exactly the view I take of it in *Viscum*.

EXPLANATION OF FIGURES IN PLATE XVII.

Illustrating Dr. Schönland's paper on the Morphology of the Mistletoe ($\it Viscum\ album,\ L.$).

[All figures represent diagrams of flowering shoots as actually observed by the author, with the exception of Fig. 9.]

[A=mother axis of each shoot; B=bract; p=prophyll; L=foliage-leaf; b=axillary bud; l=scale-leaf corresponding to L; s and s'=scale-leaves in inflorescences.]

Fig. 1. Normal female shoot (after Eichler).

Fig. 2. Normal male shoot.

Fig. 3. Male shoot in which the posterior foliage-leaf has split into two; the anterior leaf shows beginning of splitting; the terminal inflorescence is also abnormal.

Fig. 4. Trimerous female shoot.

Fig. 5. I. Trimerous male shoot; one lateral flower is not developed. II. Tetramerous male shoot; one lateral flower and the terminal flower are not developed. The two median lateral flowers are trimerous, and occupy the apex of the shoot.

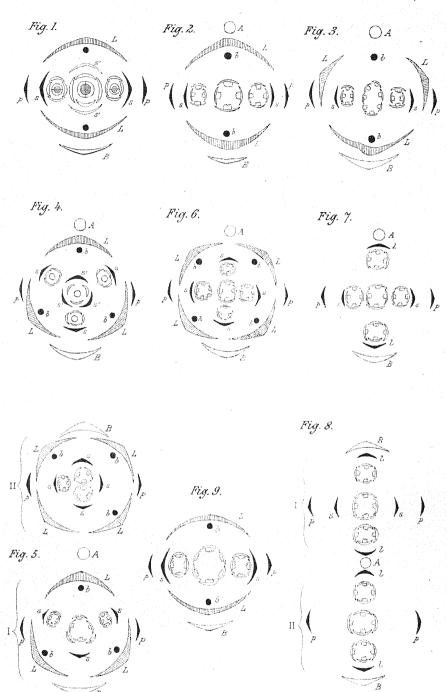
Fig. 6. Tetramerous male shoot; one lateral flower is trimerous, another pentamerous.

Fig. 7. Male shoot with five flowers developed from a dormant bud. In the place of the two foliage-leaves, scale-leaves are developed which also bear flowers in their axils.

Fig. 8. I. A similar case as represented in Fig. 7, only the two lateral flowers are suppressed. II. Case similar to the preceding one: a further reduction has taken place by the suppression of the uppermost pair of scale-leaves.

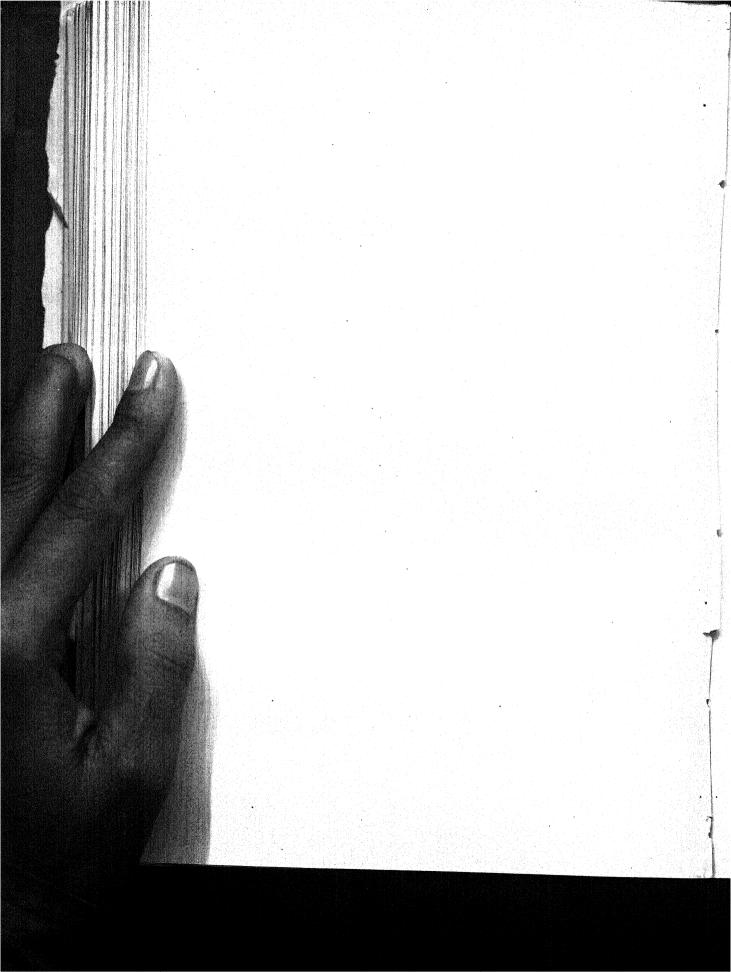
Fig. 9. Male shoot with hexamerous terminal flower (after Eichler).





Schönland del

University Press, Oxford.



Sphaerococcus coronopifolius, Stackh.

BV

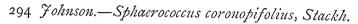
T. JOHNSON, B.Sc. (London),

University Scholar in Botany, Demonstrator of Botany in the Normal School of Science, Kensington.

With Plate XVIII.

VEGETATIVE THALLUS.

HE red sea-weed Sphaerococcus coronopifolius, Stackh., occurs, in England, along the south-west coast from the Isle of Wight to Land's End, being found attached to rocks at extreme low-water and deeper levels, by means of a disc-like 'root,' from which one to three main 'stems' arise. The main stem produces irregularly placed branches, from which very numerous short upwardly directed branchlets spring. These alternate or subdichotomously formed branchlets are flattened and relatively wide, and have the whole length of their two edges closely beset with small cylindrical filaments, often themselves slightly branched (Fig. 1). The whole plant may be a foot long, and as broad as it is long. Each cylindrical filament repeats on a smaller scale the structure of its parent branchlet, and this of its parent branch (Fig. 2). Running through the middle of the filament is a central axis consisting of a uniscriate row of large tubular cells in which the usual Floridean characters are wellmarked. From the distal end of each joint-cell of this central axis two lateral uniseriate cellular branches are given off right and left, obliquely inclined in an upward direction to the surface of the thallus-filament. Each lateral cellular branch forms a number of short secondary lateral branches arranged at right angles to the surface of the thallus, and closely [Annals of Botany, Vol. II. No. VII, November 1888.]



applied to one another, side by side, so as to produce a compact cortex, the thickness of which is increased by the apical growth of these cortical secondary lateral branches (Fig. 7). Each member of the branch-system of the thallus thus consists of three layers; a medulla formed by the central axis, a middle layer formed of the loose lateral cellular branches of the central axis, and a cortex formed as just described. The 'midrib' (central axis) and the 'lateral ribs' (lateral cellular branches) were first observed and described by Sowerby, according to Harvey1, but their relation to one another and to the rest of the thallus in the way with which Schmitz² has made us familiar in the Florideae generally, was not known. Up to the present the central axis and its lateral branches have not been figured. Most of the figures of the thallus branches published are life-size, and taken from living or dried specimens. Examination however of spirit-material treated with clearing reagents and magnified four or five times brings out the central axis and its branches well (Figs. 1 and 2).

THE PROCARPIUM.

As it is in the cylindrical filaments, the ultimate branches of the thallus, and in them only that the female sexual organs—the procarpia—occur, I shall speak of them as procarpium-branches. It is no doubt in a great measure owing to the opacity of these branches, the absence of any external indication of the presence, not to say the exact position, of the buried procarpia, the smallness of the cells, and the number of different planes in which the various parts of the procarpium lie, that they have not hitherto been even mentioned. Their number somewhat atones for their general obscurity. We have seen that the whole margin of the thallus-branchlet is beset right and left with cylindrical filaments. These are all

¹ Harvey, Phycolog. Brit. ii. pp. 182-184, Pl. 61. 1846-1851.

² F. Schmitz, Untersuchungen über die Befruchtung der Florideen in Sitzungsber. d. k. Akad. d. Wiss. Berlin, 1883. Translation by W. S. Dallas, F.L.S., in Ann. Mag. Nat. Hist., vol. xiii. 1884, in which any following references will be found.

procarpium-branches potentially. In each of them the procarpia, the number of which varies from one to six or more, occur at intervals throughout its length, close to the central axis, above, below, right or left of this as seen from above. In fact any primary lateral cellular branch of the central axis may develope a procarpium. From the second (proximal) joint-cell, rarely from the basal cell, of such a cellular branch, a usually three-celled secondary lateral branch arises. The three cells are so related to one another as to form a curved branch (Fig. 3); they are full of highly refractive minutely granular nucleated protoplasm, and constitute a carpogenous branch, the apical cell of which is the carpogonium and developes the trichogyne. This carpogenous branch is readily distinguishable from the other secondary lateral branches by lying deeper within the procarpium-branch and by the characters of the contents of its cells (Fig. 7). The procarpium is completed by the formation of a number of small secondary lateral branches of limited growth, from the basal and next joint-cell of the lateral branch bearing the carpogenous branch. These small cells, having similar but less refractive and dense contents than the cells of the carpogenous branch, are the 'carpogenous cells,' and have an important part to play in the formation of the fruit. In a longitudinal section of a procarpiumbranch seen under an inch objective, the procarpia, situated close to the central axis in the middle layer of the procarpium branch. stand out by the brightness of one or more of the cells of the carpogenous branch and by the closeness of aggregation of the small carpogenous cells. It is possible only under a higher power to make out the details of structure of any individual procarpium. Thus in Fig. 7, in the procarpium p', only one cell of the carpogenous branch could be observed under an inch objective, though under a $\frac{1}{6}$ -inch objective all the cells of the carpogenous branch as well as part of the trichogyne were recognisable. The trichogyne is unusually variable in its course in Sphaerococcus. It reaches the surface of the thallus after curving in different cases in almost every imaginable direction, sometimes creeping for a long way in the

interior of the thallus as if searching for a weak spot in the cortex, there to project on to the external surface. It is only rarely that it passes almost directly to the surface (Fig. 4). It was not until I had spent a long time in examining some hundreds of sections under a $\frac{1}{6}$ -inch objective that I could satisfy myself that the coiling filament I saw in connection with the carpogenous branch was really the trichogyne, and that it projected at the thallus surface. I was constantly cutting it across. Indeed, in making thin sections of a procarpium-branch, it is almost sure to be so cut even if the rest of the procarpium is left intact. I found it very useful to place a piece of a thallus-branchlet bearing several procarpiumbranches for twenty-four hours or more in a mixture of pure glycerine and alcohol until it became semi-transparent, then to examine each procarpium-branch on both sides with a high power until one was seen in which the procarpia were likely to yield useful results, and taking this particular procarpium-branch, after noting the exact position of its procarpia, to cut it longitudinally between thumb and finger. The sections, though sometimes lost or spoilt, were usually thin enough to allow examination of the procarpia and yet thick enough to prevent injury of them. Subsequent staining with various reagents often rendered the parts, in the usual way, more distinguishable.

THE CYSTOCARP.

I did not clearly see the contact of a spermatium with the trichogyne, but judging from changes in the procarpium it is highly probable that fertilisation takes place in the normal way. More than once I found the trichogyne cut off from the rest of the carpogonium by a constriction at its base (Fig. 5), the contents of the carpogonium being thus divided into a useless non-nucleated part (compared by Schmitz to the polar body of *Vaucheria*), and a more important nucleated part, the fertilised ovicell, the foundation of the fruit. In one case in which the trichogyne had been cut off I found two nuclei in the 'fertilised ovicell,' but whether they were the

male and female nuclei about to fuse, or were due to the division of the nucleus of the fertilised ovicell, I cannot say (Fig. 6). In another case the wall of separation between the carpogonium and the middle cell of the carpogenous branch had broken down, the contents of the two cells were completely fused together, but the nuclei were still separate. A fusion of this fused cell with the basal cell of the carpogenous branch I did not observe with certainty. There is, I think, little doubt that it occurs. Investigations of later stages of development gave some very interesting results which show the necessity of the examination of each genus of the Florideae. The course of events in the development of the cystocarp in Sphaerococcus is briefly as follows. The carpogonium (after fertilisation) fuses with the hypogynous cell, and this apparently fuses with the basal cell of the carpogenous branch. The common cell so formed next fuses with the mother-cell of the carpogenous branch, the second (proximal) joint-cell of a lateral branch, and this cell then fuses with the basal cell of the same branch. Fusion however does not cease at this point, for the basal cell of the lateral branch fuses with the cell bearing it, a joint-cell of the central axis of the procarpium-branch, and this joint-cell fuses with the next jointcell below it. By this means a large common conjugation-cell is obtained, from the greater part of the surface of which (not from that part formed by the two joint-cells of the central axis) ooblastema-threads arise even before the process of fusion is completed. These threads are short radiating, branching, and of few cells, the end one or two cells becoming carpospores. It has been seen that each procarpium is completed by a cellcomplex of carpogenous cells borne by the two basal cells of the primary lateral branch concerned. These carpogenous cells do not remain sterile here. They become more directly connected with the common fused cell, the central cell of the cystocarp, and produce at their free ends chains of carpospores just as do the ooblastema-threads directly sprouting from the central cell. Carpogenous cells similar to these have been described in other genera, and have had ascribed to them a similar

function. Schmitz states that a closer investigation of their fate shows them to be sterile and not connected with spore-formation. This conclusion will throw doubt on the accuracy of my statement. Still all the observations I have made in *Sphaerococcus* support my view, and in addition it should be stated that in no other genus of the Florideae (*Gracilaria* excepted) is a fusion of the individual cells of a procarpium known to take place to such an extent 1.

As the development of the fruit proceeds its size increases until there is a clear indication to the naked eye of its presence, in the form of a spherical swelling. As a fruit may arise from any one of the procarpia scattered through the whole length of a procarpium-branch, and as this branch may be quite short when fertilisation occurs, it is easy to explain the earlier descriptions of the cystocarp of Sphaerococcus taken from an external examination of the plant. 'Fructificatio, tubercula minutissima, modo sessilia, modo pedunculata, in ramulis extremis sita, atro-purpurea2.' The fruit-sheath (pericarp or involucre) is derived from the cortex of the procarpium-branch, and is thus present before the fruit begins to form. The fruit-cavity is a result of the arching of the pericarp and of an increase in the distance between the lateral cellular branches of the joint-cells of the central Lysigeny does not occur, schizogeny strictly speaking occurs to only a limited extent; the fruit-cavity is due rather to the increase of the space between the cellular branches which have been free from one another at their

¹ Schmitz, op. cit., p. 23, says, 'Perhaps, also, in some of these forms (Rhodomeleae) a plurality of auxiliary cells may be formed in the individual procarpium; but I have hitherto never been able to demonstrate such a case with certainty.' Again, in a footnote on p. 20, Schmitz says: 'This point [the conjugation of the fertilised ovicell with the nearest auxiliary cell] in the development of the fruit of the Corallineae (the exact investigation of which is, as is well known, rendered remarkably difficult by the small size of the cells), I have hitherto been unable to establish directly. Moreover, not only in the Corallineae, but also in many other Florideae with small-celled, closely packed cellular tissue, there are special difficulties opposed to the exact ascertainment of the fate of the fertilised ovicell which render these investigations extremely troublesome and tedious, and greatly hinder any certain decision.'

² Good. and Woodw., in Trans. Linn. Soc. iii. p. 185.

proximal ends from the first. The carpospores escape from the ripe fruit through an irregular slit in the pericarp, not through a definite pore. On account of the frequent formation of a fruit-cavity of large size, especially towards the apex of the procarpium-branch before there is any indication of carpospores, the size of a swelling is not a safe guide as to the stage of development of the fruit. Each cystocarp is the product of one procarpium and of one only, close as the procarpia are to one another and loose as is the middle layer of the procarpium-branch. The carpogonium has in its immediate neighbourhood a number of cells, some of which are specialised, and with all of which it fuses to produce the central cell of the cystocarp. All these cells are auxiliary cells, and being close to the carpogonium do not need any ooblastema-thread (connecting-tube) to place them in connection with the fertilised ovicell. able to throw much light on the fate of the nuclei in these auxiliary cells, and cannot say how far their fusion with one another, following on that of the hypogynous cell with the carpogonium, should be regarded as a second act of fertilisation (granting this may happen), here many times repeated. Looking at the development of the cystocarp from another point of view, Sphaerococcus exhibits the phenomena of fecundation as seen in the Florideae at their best. In no other genus in which one cystocarp results from one procarpium is the possibility of the abundant supply of nutriment from a number of different regions in the thallus to the central cell of the cystocarp and so to the sporigerous filaments insured to such a degree. In Sphaerococcus, not only does the carpogonium fuse with the other cells of the carpogenous branch, but with the two basal cells of a lateral branch and with two joint-cells of the central axis of the whole procarpium-branch. The nearest approach to this (after Gracilaria) is seen in Chondria tenuissima, Ag., one of the Rhodomeleae. In this species 1, after fertilisation, the

¹ Schmitz, op. cit., p. 28.

auxiliary cell which is the mother-cell of the carpogenous branch and bears in addition a cell-complex, fuses with the carpogonium, and with the nearest cells of the cell-complex, giving a large multinucleate cell from which sporigerous filaments sprout out. In Sphaerococcus there is a combination of the three chief types of fruit-formation of the Florideae; for the ooblastema-threads arising from the surface of the carpogonium are comparable to the sporigerous filaments of the Helminthocladieae (Némalion, Batrachospermum, etc.), and those from the surface of the fused auxiliary cells and from the carpogenous cells (secondary auxiliary cells) are comparable to the sporigerous filaments of the Rhodomeleae and other Florideae with more or less compact thallus, and to the sporigerous filaments (meta-ooblastema-threads) of the Squamarieae and Cryptonemiaceae. A comparison of the course of development of the fruit in Sphaerococcus with that in Gracilaria will show how very similar these two genera are in this respect. Comparison of the vegetative thallus of the two shows Sphaerococcus to be the less modified form. In Gracilaria the central axis of the thallus branch is no longer evident, since its lateral branches are as well-developed and have applied themselves closely together and to its sides, forming a central medulla of large cells in which the jointcell of the central axis is obscured. The absence of a clearly marked central axis in S. australis Harv. caused Harvey 1 to exclude this plant from the genus Sphaerococcus and to place it nearer Gracilaria. Opinions differ as to the other genera to be included in the Sphaerococcaceae. Schmitz² considers Nitophyllum to be a member of the family and describes its procarpia as being the simplest. Its thallus is very different from that of either Sphaerococcus or Gracilaria, and its fruit, judging from the brief account of Schmitz, is not at all like that which I have described in these two genera. Hauck 3 considers Chondrymenia to be the third genus of

¹ Harvey, op. cit.

Schmitz, op. cit., p. 24.
 Hauck, Rabenhorst's Krypt.-Flora, Die Meeresalgen, 1885, p. 184.

the family. Its thallus is readily conformable with that of Sphaerococcus, though its procarpia and fruit-development are not yet known. Kützing¹ describing S. coronopifolius as mentioned under the name Rhynchococcus, places Rhynchococcus with Calliblepharis in the family Rhynchococceae. If the latest view, that of Schmitz, be followed and the genus Nitophyllum be regarded as one of the Sphaerococcaceae, this family presents a striking example of the difficulty of determination of the exact systematic position of a genus from a consideration of the structure of its thallus; for in these three genera we have examples of three of the four main types of thallus-structure met with in the Florideae:—

1. In the simplest Florideae (many of the Helminthocladieae) there is a uniscriate cellular central axis with apical growth and bearing numerous free lateral radiating branches. This type is not represented in the Sphaerococcaceae.

2. The lateral branches (also uniseriate, cellular, branching, and apically growing) have become more or less closely applied to one another so as to form a loose cortex to the distinct central axis. This type, seen in the Gelideae and Rhodomeleae (e.g. species of *Polysiphonia*), is represented by *Sphaerococcus*.

3. The lateral branches are closely applied to, and as well-developed as, the central axis, which is no longer distinguishable as such (Corallineae). Represented by *Gracilaria*.

4. The lateral branches are closely applied to one another, and occur right and left of the parent axis in one plane, essentially giving the thallus a flattened parenchymatous character (some of the Rhodymenieae). Represented by *Nitophyllum*.

Supposing the accounts of the structure of the procarpia and of the development of the cystocarp in *Sphaerococcus* and *Gracilaria* to be correct, I still refrain from any attempt to assign to them any other position than that they at present occupy, hoping that when more genera have been examined

¹ Kützing, Phyc. Gen., p. 403 (1843).

and the systematic arrangement of the Florideae is undertaken afresh, the results of the present investigations may

prove useful.

It remains for me to compare the present account of Sphaerococcus coronopifolius with that of previous observers. According to Harvey 1 the plant was first noticed by Ray and described by him in his Synopsis 2. Sowerby, as already noted, was the first to observe, with the aid of the simple microscope, the 'midrib' and faint veins of the thallusbranches. Goodenough and Woodward in a paper read before the Linnean Society in 1795, 'Observations on the British Fuci, with particular descriptions of each species,' described S. coronopifolius as Fucus coronopifolius³. Their description of the fruit has been already quoted. In 1801 Stackhouse's work on Marine Plants 4 was published. In this treatise Stackhouse objects to the wide range of forms included in the genus Fucus, and suggests amongst other new genera Sphaerococcus, the generic diagnosis being 'external globular pericarps adnate or immersed; sessile or pedunculate; containing seeds as above.' Stackhouse continues: 'This forms a very numerous genus, as many of the larger shrubby species and almost all the minuter kinds are found to be tubercled, and it does not appear to me that the tubercles being sometimes internal is a sufficient reason to separate them from this genus, as it may arise either from accident or from the plant not being sufficiently advanced in maturity.' The latter theoretical alternative is seen to be practically true. Speaking of the fructification, Stackhouse says: 'The fructification of this species is subject to vary; in its luxuriant state the margin is fringed with soft forked branching spinules, among which the orbicular seed-bearing tubercles are intermixed like berries. It seems however at times to have simple pedunculate tubercles on the margins.' The description is accompanied by a colored illustration of

Harvey, op. cit.
 ² Ray, Synopsis.
 ³ Good. et Woodw., op. cit. p. 185.
 ⁴ Stackhouse, Nereis Brit. 1801, p. 83, Pl. XIV.

the fruiting thallus (natural size). Harvey 1 describes the branches as 'multifid ending in acute laciniæ [branchlets] fringed with cilia [procarpium-branches], tubercles [cystocarps] immersed in the cilia.' The first biologist who gave any details of the internal structure of the cystocarp was J. Agardh2, and in these words: 'Coccidia . . . nucleum simplicem foventia; placenta basalis cellulis strati medullaris contexta, a vertice et lateribus fila gemmidiifera ima basi subfasciculata.' Kützing 3 in 1843 was the first and only observer who figured the internal structure of the cystocarp. In this figure, repeated in Kützing's 'Tabulae Phycologicae4' and in Hauck's5 'Die Meeresalgen,' taken from a transverse section of the fruit, the sporigerous filaments are represented radiating from a central placenta of numerous small cells. There is no indication of the very large fused 'central cell' which I have described. It looks very much as if Kützing's figure was made from a transverse section of the fruit beyond the point of origin of the sporigerous filaments from the central cell and in the region of the 'carpogenous cells.' The procarpia have not hitherto been observed.

I am very much indebted to Dr. D. H. Scott for the suggestion of the investigation, for the supply of the material, and for opportunities of examining it.

¹ Harvey, op. cit.

² J. Agardh, Sp. Alg., iii. p. 395.

³ Kützing, Phyc. Gener., p. 403, Tab. 61. I.

⁴ Kützing, Tab. phyc. xviii. Tab. 10.

⁵ Hauck, op. cit., p. 179, Fig. 76 b.

304 Johnson.—Sphaerococcus coronopifolius, Stackh.

EXPLANATION OF FIGURES IN PLATE XVIII.

Illustrating Mr. Johnson's paper on the procarpium and fruit in Sphaerococcus coronopifolius (Stackh.).

Fig. 1. A piece of the fruit-bearing thallus. cys. cystocarp. p.~b. procarpiumbranch. \times 4.

Fig. 2. The small piece, a, of Fig. 1 more highly magnified. Letters as before \times 40.

Fig. 3. A procarpium (except carpogenous cells). c. carpogonium. h.c. hypogynous cell. c.l. cells of lateral branch. c.s. cells of central axis. t. trichogyne projecting at right angles to plane of vision. \times 1000.

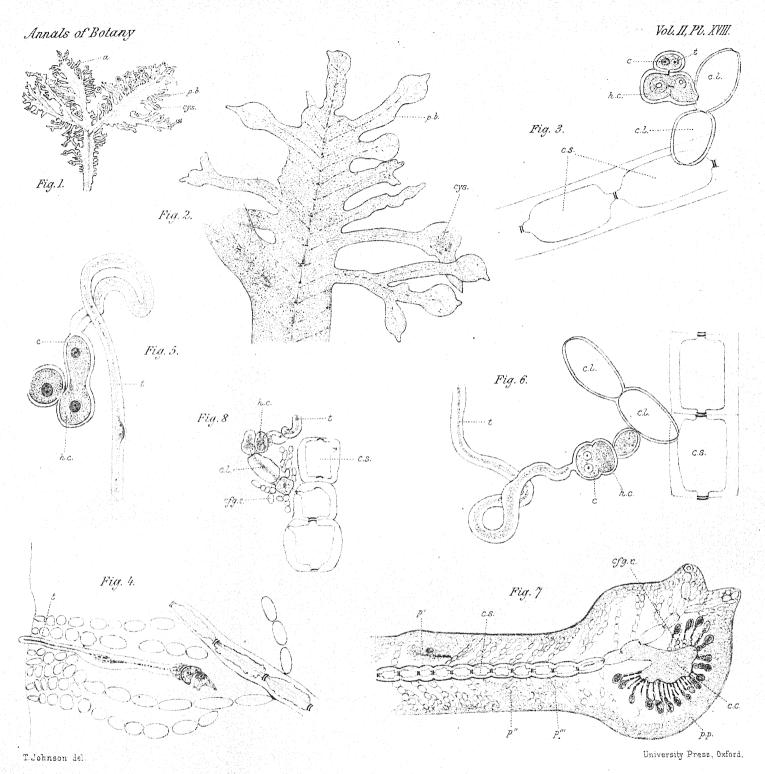
Fig. 4. A part of a procarpium-branch. t. trichogyne projecting. × 480.

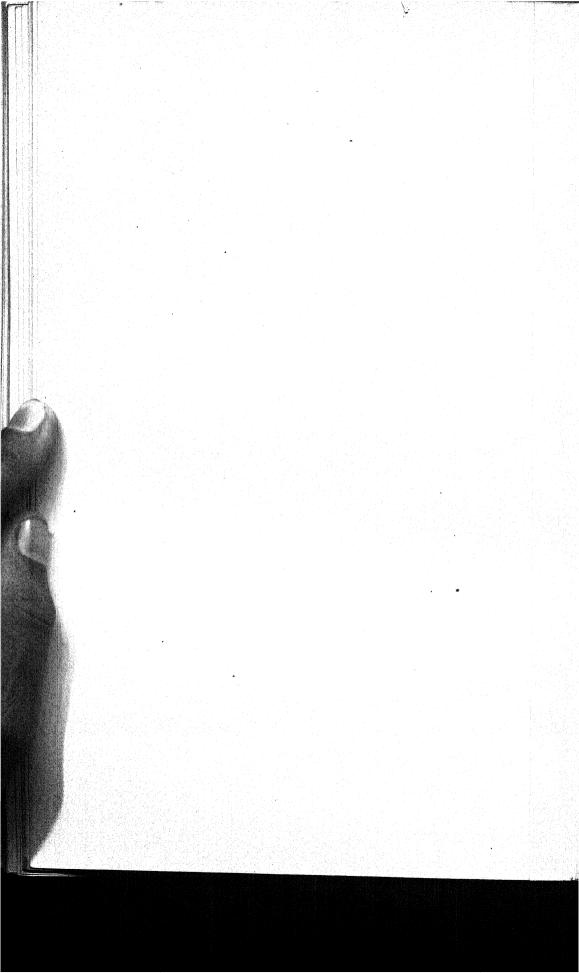
Fig. 5. Beginning of cystocarp. Carpogonium, c., and hypogynous cells, h. c., fusing. t. trichogyne cut off. \times 1000.

Fig. 6. Part of a procarpium just after fertilisation. In the carpogonium, ϵ , are two nuclei. Other letters as before. \times 1000.

Fig. 7. Longitudinal median section of a procarpium-branch. c.s. joint-cell of central axis. p'p''p''' three procarpia; efg.c. the carpogenous cells. In p' the cells of the carpogenous branch and a little of the trichogyne were visible under a q-inch obj. In p''' the greater part of the trichogyne was observable, the cells of the carpogenous branch were found in another section. e.c. the fused central cell of the fruit, showing radiating ooblastema-threads. pp pericarp or involucre (fruit-sheath). x 120.

Fig. 8. Part of a procarpium (p', of Fig. 7), showing some of its carpogenous cells, egg. c. Other letters as before. \times 400.





On the foliar organs of a new species of Utricularia from St. Thomas, West Africa.

BY

H. N. RIDLEY, M.A., F.L.S.

With Plate XIX.

N examining a small epiphytic species of Utricularia, sent me by Professor Henriquez, of Coimbra, from St. Thomas' Island, I observed that it possessed spathulate leaf-like bodies resembling those of several other species. They were narrow and filiform at the base, broadening into a lamina about one-sixteenth of an inch in diameter, and apparently had been green in colour with three veins. Most of them had lost the apex, but in one specimen the body was terminated by a slender filiform process bearing utricles. Further examination showed that every stage occurred between the slender filiform process frequently branched and bearing numerous utricles and the flattened leaf-like lamina. In slightly expanded and flattened processes it was easy to see that the utricles sprang from their edge only and were not scattered over their surfaces; further, in the case of one branched process, while one ramus was flattened and leaf-like, the other appeared slender and utriculiferous. The most completely leaf-like bodies bore no utricles upon their edges, but where there was only a slight flattening the utricles occurred.

A similar modification was figured by Professor Oliver¹, in *Utricularia Jamesoniana*, a small epiphytic species from the

¹ Journal of the Linnean Society, vol. iv.

[Annals of Botany, Vol. II. No. VII. November 1888.]

Andes, and apparently allied to the one I describe below; but he seems to have considered the spathulate leaves ending bluntly as quite distinct organs from the flattened bodies bearing utricles along their edge. I have seen the specimens of *U. Famesoniana* in the Kew Herbarium, upon which Professor Oliver based his drawings, and find them exactly as figured. In them the two members seem at first sight different, but from our African specimen it would appear that they are really of the same nature, and are merely forms of the same member modified for different uses.

If this be the case doubt may well be thrown on the foliar nature of these leaf-like bodies. For though they are somewhat regularly arranged on the little tuber from which they spring, yet as they are able to branch irregularly, some of the branches becoming spathulate leaf-like bodies with three nerves, and others remaining as utriculiferous threads, it seems impossible to consider them leaves, and they should rather be regarded as of the nature of stem-structures¹. This view is confirmed by the African plant, in which one of the utriculiferous threads bears a small tuber, similar to the one from which it has sprung, at its apex, which again has emitted threads (Fig. I A).

It is clear that an organ which can elongate and branch irregularly, and eventually produce a tuber, cannot be anything but a stem-structure. Hence it would appear that in the epiphytic species of *Utricularia*, at least, these leaf-like bodies are dilated phylloclades.

 $U.\ bryophila$, n.sp. Planta humilis muscicola, tubere minuto. Phyllocladi longe petiolati, petiolis linearibus angustissimis, semiuncialibus, laminis loratis $\frac{1}{2}$ uncia longis $\frac{1}{16}$ uncia latis, apicibus longis filiformibus, utriculiferis, $\frac{3}{4}$ uncia longis, vel ultra interdum ramosis. Utriculi pauci minimi. Scapus $\frac{1}{2}$ uncia longus scabridus. Bracteae lanceolatae acutae paucae.

¹ I have added to the Plate a sketch of an utriculiferous thread from Utricularia pusilla, a Ceylon species, in which one branch is similarly converted into a spathulate phylloclade. I believe it to be a constant occurrence in many other species, but in herbarium material is not very easy to make out, owing to the fragility of the threads when dry.

Flores singuli majusculi flavi $\frac{3}{4}$ uncia longi pedicellis scabridis. Calycis lobus superior ellipticus ovatus obtusus. Corollae labium superius bifidum dentibus duobus acutis recurvis, labium inferius latum trilobum ferme $\frac{1}{2}$ uncia latum lobi laterales rotundati quadrati lati, obtusi, medio longiore recti obtuso. Calcar pedicello ferme aequale abrupte truncato.

St. Thomé ad 1300 ped. alt. inter muscos apud arbores. Leg. Moller, Com. Prof. Henriquez.

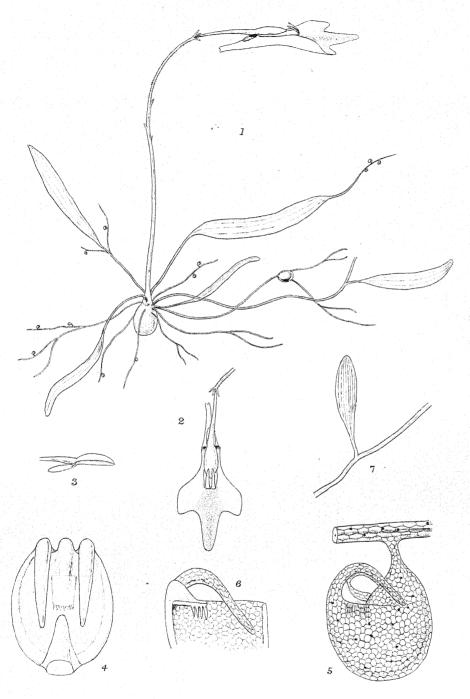
The flowers seem to have been bright yellow, with a very bright band down the centre. The utricles are small and scanty, as is often the case in the epiphytic species of *Utricularia*. They are globose, and shortly stalked, and there are two horns which, arising from the outer margin, are curved down over the opening of the utricle, and between them a smaller process lies which bears on the inner end a small flat plate armed with little teeth.

DESCRIPTION OF PLATE XIX.

Illustrating Mr. H. N. Ridley's paper on the Foliar Organs of a new species of *Utricularia* from St. Thomas.

- I. Utricularia bryophila, n.sp. Twice natural size. A. Tuber borne on a rhizome.
- II. Flower from above, enlarged.
- III. Calyx.
- IV. Utricle, much enlarged.
- V. Mouth of utricle from above.
- VI. Section through the utricle, showing the plate with teeth.
- VII. A branch bearing a phylloclade of U. pusilla from Ceylon.

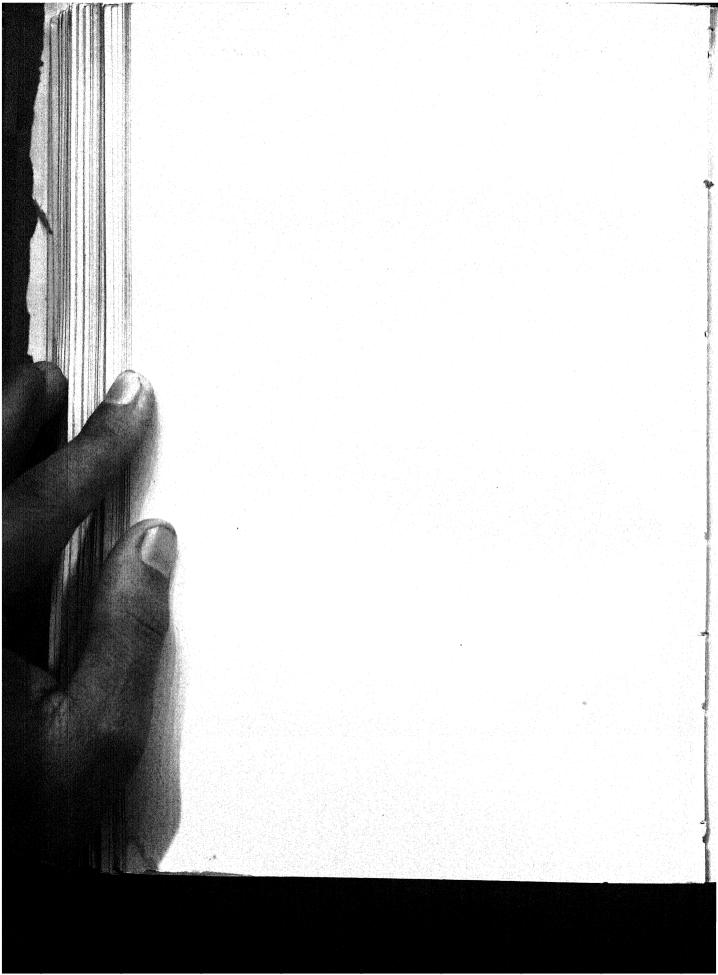




Berjeau & Highley del.

University Press,Oxford.

H.N.RIDLEY .- ON UTRICULARIA BRYOPHILA.



On the Floral Organogeny and Anatomy of Brownea and Saraca.

BY

MARCUS M. HARTOG, D.Sc., M.A., F.R.U.I.

With Woodcuts 14, 15, and 16.

THE Caesalpinieae have been scarcely investigated from any but a purely systematic point of view; a study of the floral ontogeny of Cassia by Rohrbach¹ and of Amherstia by Griffith² are the only two extant. The free flowering of several specimens of Brownea coccinea, B. grandiceps, and Saraca indica, L. (Fonesia Asoca, Roxb.) in the plant-houses of Queen's College, Cork, has led me to investigate these two closely allied genera with a view to fill up a gap in our knowledge. Both genera belong to the group Amherstieae, characterised by the excentric position of the gynaeceum on the posterior lip of the calyx-tube next the vexillary petal, and with the dorsal suture towards the tube.

Brownea coccinea (from which B. grandiceps differs in no essential point) has shortly stalked flowers in short capitate racemes, often from defoliated axils and on the old wood. The lower bracts are distichous and equitant when young, empty or with their axillary flowers developing late; the upper are narrower, spathulate, arranged in a $\frac{3}{8}$ spiral, and all axillant to flowers. Each pedicel bears two closely connate bractlets forming an obconical sac, opening by an apical slit (antero-posterior). The flower shows only four sepals, owing to the connation of the posterior pair; allowing for this they

¹ Bot. Zeit. 1879.

² Notulae.

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imbricate quincuncially (sep. 1 antr.). The four sepals become free at the rim of the long floral tube, on which are also inserted the five (variably) imbricate petals, not markedly heteromorphic or unequal, and nine or eleven 1 stamens monadelphous, the long erect tube split to the base on the posterior (vexillary) side. The solitary carpel has the normal orientation of the Leguminosae, its dorsal suture being anterior, its placenta posterior; its stipe is adnate as a ridge to the posterior edge of the floral tube, and becomes free at the posterior edge just within the vexillary petal.

Saraca has the calyx, gynaeceum, and floral tube of Brownea; but it is free, only slightly equitant. The flower is always apetalous, and has only the seven anterior stamens, which are free to their base; an eighth sometimes occurs, it is then posterior. The inflorescence is a stiff panicle twice or thrice branched, from the old wood. The bracts of the base of the main peduncle are distichous, but higher up they are spiral with the divergence $\frac{3}{8}$ as they are (with antidromy) on the secondary and tertiary axes. The upper bracts of the primary and secondary branches and all the tertiary are axillant to flowers.

I. THE FLORAL DEVELOPMENT OF BROWNEA AND SARACA.

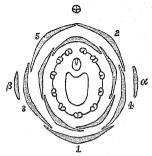
The young inflorescences of *Brownea*, like so many closely-packed racemes, contain flowers nearly of the same age. These appear first in the axils of the lowest of the spiral bracts, and follow in rapid basifugal succession, the main axis often bearing finally a terminal flower. The lower floral bracts occasionally bear flowers, which, however, take origin much later than those in the axils of the spiral bracts. The bractlets appear right and left in quick succession, one a little before the other. They soon become connate, i. e. their bases are confluent and rise up so as to form a bag of truncated

¹ Ten is a very rare number to find; eleven is commoner in *B. coccinea*, nine in *B. grandiceps*.

conical form, with only a median slit at the apex, the margin of the older (Fig. 14, a) bractlet overlapping the other (Fig. 14, β). Within this sac the receptacle has widened and become obconical, somewhat tilted outward, so that the rounded upper surface, covered by the slit of the bracteolar sac, looks towards the hollow of the bract; hence in *Brownea* we have not the same marked difference of pressure between the anterior and posterior sides of the flower that usually prevails at this stage in closely-packed inflorescences. The sepals appear in quincuncial order; sepal I is anterior (see

Fig. 14), 2 postero-lateral on the side of bractlet α , 3 antero-lateral on the β bractlet side, 4 antero-lateral on the α side, 5 postero-lateral on the β side again; 2 and 5 early become confluent at the base; but the resulting posterior member is long, unequally divided by a notch into a larger portion corresponding to 2, and a smaller to 5.

The petals arise as a simultaneous whorl, and so do the alternipetalous outer stamens. At this stage the swollen centre of the floral re-



the alternipetalous
At this stage the

At this stage the

At this stage the

ceptacle has become excentric to the flower, coming close up to the base of the vexillary petal behind. Hence we usually find in *B. grandiceps* only four antipetalous inner stamens, there being no room left for a posterior stamen before the vexillum; in *B. coccinea*, however, two are formed here; we may regard this as a true case of chorisis due to the pressure of the gynaeceal tubercle. This now rises up as a horseshoe with its limbs closely approximated behind. The staminal sheath forms late, and so do the receptacular tube and gynophore.

In Saraca the bractlets soon overlap above the young receptacle, on the side of the bract, but leave a small gap at the posterior side of the flower until the appearance of the sepals; they never become connate, though a overlaps β on

the posterior as well as anterior side of the flower. The receptacle is nearly erect, not tilted outwards. The calyx develops as in *Brownea*, but the confluence of the sepals, 2 and 5, is earlier and more complete. I have failed to see any sign of petaline tubercles. The stamens appear in ascending order in an antero-posterior direction in rapid succession. First, an anterior stamen, then the pair next to it, then another pair, and then another; between these, on the posterior side of the flower, is seen a narrow ridge which soon shows three minute tubercles; the middle one may enlarge somewhat, but their identity and presence are soon lost to view. At the time that there are five stamens, the central tubercle shows a slight annular margin which almost immediately becomes horseshoe-shaped owing to uneven growth; this is the carpel.

Now the important point in the above developments is, that in two closely allied genera the flower of the one develops as one would say 'normally,' by successive whorls, and in the other genus there is a marked acceleration of the anterior side. Considering the flowers of these two genera alone, it might be thought that Saraca, the more modified form of the two, with its apetalous flowers and reduced androecium, owed to these points a distorted ontogeny. This conclusion, however, is unsustainable. In all Leguminosae hitherto studied, including the actinomorphous Mimoseae, the flower is known to develop from below upwards, with the appearance of the parts next the bract accelerated, those next the inflorescenceaxis retarded. In this order then Saraca is normal, Brownea is exceptional; and it is the eucyclic development of Brownea which calls for explanation. We must, therefore, regard this eucyclic development as secondary, and hold that a reversion has taken place here, conditioned by the nearly actinomorphous relations of the adult flower. With this is correlated the peculiar position of the flower-axis (at right angles to the inflorescence-axis) at the stage when the flower-leaves make their first appearance.

It is obvious that the flowers of most Leguminosae must

rank as dorsiventral structures, while in Brownea they are, by adaptation or reversion, radial structures. Suppose now that the flower-leaves themselves were caulomes, not phyllomes; then, taking for our guide the aphorism that development, i.e. ontogeny, can alone elucidate the true nature of a structure, we should be constrained to refer the development of the flower in the two species to different types of branching. Now I do not see how the substitution of phyllome for caulome can modify the validity of the precept. If we regard the scorpioid inflorescence of a Cordia as morphologically different from that of a Borago, that of one species of Urtica as different from that of another, we must admit that the flower of Brownea is morphologically different from that of Saraca, Cassia, Mimosa, and every leguminous flower that has been studied; and herein we have a reductio ad absurdum of the above aphorism.

II. THE DISTRIBUTION OF THE FLORAL LEAF-TRACES IN BROWNEA AND SARACA.

This was the next problem to attack in order to see if it would shed any light on the morphology of the floral tube; but I soon discovered that the anomalies presented needed themselves to be explained before they could be utilised to explain other difficulties.

1. The bractlets. The arrangement in Saraca presents no difficulties. The fibro-vascular cylinder of the pedicel below the bractlets consists of six little arcs, two anterior, two posterior, and one on either side. The lateral arcs detach themselves at the node to go one to either bractlet, the one to the lower bractlet at a slightly lower level; in other words, each bractlet sends down a single leaf-trace which enters the cylinder at the extremity of the lateral axis.

In Brownea the bractlets send down numerous traces which are inserted uniformly at equal distances all round the pedicel. We must regard this distribution as a mere matter of convenience as it were; for, considering the development of the bracteolar sheath, the general occurrence of paired bractlets

in other orders, the close kinship with *Saraca*, we are constrained to admit that the uniformity of size and distribution and the number of the bracteolar leaf-traces in *Brownea* still do not justify us in regarding the sheath as composed of more than two connate bractlets.

2. The flower proper.—The easiest way to describe the distribution of the floral leaf-traces is perhaps to follow them from below upwards. In Saraca the vascular ring above the bractlets assumes a very irregular shape, with nine angular prominences, and as many bays, the posterior bay being the largest. The apex of each of the angles becomes detached

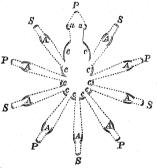


Fig. 15. Diagram to show the arrangement of the leaf-traces in the flower of Brownea coccinea. The dotted lines show how they unite edge to edge in their descent. S, sepal; P, petal; A, stamen (of the 9 anterior); a, stamen derived from the chorisis of the one in front of the vexillum; c, traces of the carpellary stipe.

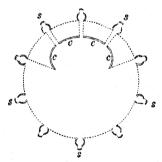


Fig. 16. A similar diagram of Saraca indica; the traces of the missing petals are present, but the small anterior traces of the carpellary stipe are absent; and so are those of the anterior stamens.

as the trace of a flower-leaf, sepal or (suppressed) petal, excluding the vexillum. The flanks of each of the seven anterior prominences separate from their neighbours and converge first on the outer and then on the inner side to form crescentic or concentric bundles for the stamens. The outer flank bundles of the two posterior angles now move inwards with a rotation on themselves, and soon, with the posterior bay, constitute a new (broken) vascular ring wholly posterior to the cavity

of the tube, which is now visible. A little higher up the ring at the posterior side of the flower gives off three bundles: one posterior for the (absent) vexillum, two lateral to the two posterior staminal rudiments (mostly undeveloped) in the adult flower; the two latter are inconstant. The lateral gaps soon close up, but the posterior is continued upwards as the gap of the ventral suture of the carpel. To state the case in other words:—the leaf-trace of the carpel forms a horseshoe with the opening posterior. The trace of the (absent) vexillum closes this gap, and the two posterior staminal traces enter the sides of the cylinder thus formed. Lower down the cylinder opens out on its anterior side; and the posterior arc so formed receives in its flanks the insertion of the traces from the posterior sepals (2 and 5). The traces of the remaining nine stamens are concentric above; below each opens into two, and between the two of each stamen is inserted the trace of one of the remaining sepals or petals. In the upper part of the tube the leaf-traces of the sepals and (absent) petals branch collaterally and approximate irregularly, so that each leaf receives a number of bundles.

In Brownea the arrangement of the bundles is also a ninepointed festoon with the odd bay posterior. The points go to the nine anterior flower-leaves, i.e. to the sepals and the four anterior petals. The flanks of each of the seven anterior cusps bend inwards, and converge in pairs to the seven anterior stamens. The remaining small bundles, one from each of the six anterior bays, cross obliquely towards the back of the flower, and form a crescent open behind for the posterior part of the gynophore; the flanks of the two anterior cusps also converge to form each a posterior staminal trace, smaller than the seven anterior. The posterior bay now becomes convex behind, and with the large bundles from the two adjacent bays and the crescent formed of the six small bundles from the lateral and anterior bays, forms a circle at the posterior side of the flower, separated from the excentric arc of the seven more anterior staminal traces by the opening of the tube. Higher up the vexillary trace (flanked by two small crescents for the tenth and eleventh stamens in B. coccinea) separates from the rest of the circle which is continued in the gynophore. In other words, each staminal trace splits into two 'half-traces,' which are inserted on either side of the corresponding sepaline or petaline trace; with the exception that when eleven stamens are present, the traces of the posterior pair go without splitting to either side of the vexillary trace. The traces from the gynophore are inserted between the 'half-traces' of adjacent stamens, from this point of view the two posterior of eleven stamens behave as 'half-traces'; the anterior traces from the gynophore are smallest.

Further, we must note that irregularities often occur; especially that the small traces of the gynophore from the seven anterior stamens may be much reduced, and I think in some cases absent.

Let us see what morphological light we can get from this study. First of all, *Saraca*, though apetalous, is equipped with a full set of alternisepalous traces obviously equivalent to the petaline traces of *Brownea*. Here we have evidence of the phylogenetic abortion of the petals, such as could not have been gleaned from the ontogeny. Again the double nature of the posterior sepal in both genera is confirmed. Then the congenital chorisis of the two posterior stamens (completing eleven) in *Brownea coccinea*, inferred from comparison with other Leguminosae, is confirmed by the fact that either sends down a single trace to be inserted on one flank of the vexillary trace; the others send down a trace which divides into two 'half-traces,' going to either flank of a floral leaf-trace.

All this is plain sailing; but it is otherwise when we look at the gynophoral traces of *Saraca*, taken by itself.

Here the stipe of the pistil receives its traces only from the posterior side of the vascular cylinder of the pedicel; in other words, they enter between those of the other floral organs of the posterior side only. If we consider the stipe as an internode between the stamens and pistil, it is obvious that its components should be inserted symmetrically between those of the lower verticels. If, on the contrary, with Karl

Schumann, we regard it as the petiolar base of the carpellary leaf, since the carpel is certainly anterior, its bundles should join those of the anterior organs. Taken alone, the distribution of the leaf-trace bundles of *Saraca*, instead of shedding light on the morphology of the gynophore, presents an enigma for solution.

In Brownea and the Proteaceae we find an explanation of the enigmatical conditions of Saraca. The proteaceous flower has a four-leaved perianth with antiphyllous stamens; and a single stipitate carpel with its placenta posterior—consequently the carpel itself is anterior, as in Saraca, Brownea, and the other Amherstieae. In some species the flower is actinomorphic; in others the perianth is open to the base in front, gamophyllous and gibbous towards the back, so as to form a short tube on the side next the ventral suture of the carpel. not the dorsal as in Amhersticae. In the actinomorphous species I have examined the leaf-traces of the gynophore are inserted symmetrically; in the zygomorphous we may distinguish two cases. In some (Grevillea spp.) the leaf-traces from the posterior side of the flower are present, but weaker; in the other case (Stenocarpus salignus) they are absent, and the bundles are exclusively derived from the anterior side of the flower. A judgment founded exclusively on the flower-anatomy of such a flower would say that the carpel being anterior received its bundles from the anterior side of the flower; but the case of Saraca, where the stipe of the anterior carpel receives all its traces from the posterior side, prevents this easy solution.

But the true conditions are obvious; the excentric position of the stipe, owing to the formation of the flower-tube, has influenced the internal anatomy. With the tube posterior, the posterior bundles are reduced or absent, as in Proteaceae 1; with the tube anterior, the anterior leaf-traces are reduced (Brownea) or absent (Saraca).

¹ From examination of some specimens of a *Bauhinia* kindly sent by Prof. Oliver, I believe the conditions are the same as in *Stenocarpus salignus*, the tube being anterior to the adnate stipe; but I failed to obtain satisfactory preparations from the dry material.

The presence of a complete or only partially reduced cycle of traces in the stipe of Proteaceae and *Brownea* would seem to favour the view that this is really the prolongation of the floral axis, and not a petiolar organ.

All the evidence is consistent with the view that the flowertube is a hypertrophy of the cortical zone of the axis through which the leaf-traces bend outwards to their leaves.

In conclusion, we may note that this research, limited as its field has been, has shown the inadequacy of any single method or criterion of morphological research. I have striven to follow in the footsteps of our regretted master, Eichler, and to seek on every side evidence as to the modifications and filiation of structures which we are compelled to regard as having a common origin, and to reject all conclusions that ignore this necessary filiation.

One word as to technique. For development I have worked mostly with the simple microscope and spear-headed needles, using sections of developing buds, and the compound microscope only to elucidate one or two difficulties, and especially to verify the exact phyllotaxis of the floral bracts. I have found a most useful adjunct to my outfit in Nobbe's germinator, a thick block of porous pottery with a central disc surrounded by a gutter for water, and provided with a cover. On the disc the buds keep fresh for many days in a cool room; and a bud half dissected at night has remained in good condition till next morning. The only necessary precaution is that the disc should not be wet, only damp, as wet accelerates the browning and softening of the flowers in their meristem state.

The distribution of the vascular bundles has been chiefly worked out by moderately thick transverse sections treated with ammonia and glycerine, and sketched under the camera. For this purpose I have found the adjustable objective a* Zeiss invaluable.

A lily-disease.

BY

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With Plates XX, XXI, XXII, XXIII, XXIV.

OR several years past I have been greatly interested and puzzled by a certain type of small discoloured spots on the leaves, stems, and other parts of various plants, and during the summer of 1886 I had frequent opportunities of noticing a particular class of these discolourations in the form of orangebrown and buff specks which appeared on the stems, pedicels, leaves, and buds of the white lily (*Lilium candidum*) growing in my garden. Some attention was also paid to them by me in 1887.

These spots, similar to those on the bracts in Fig. 1, and on the bud in Fig. 2, perplexed me exceedingly for a long time, and it seemed as though they would have to be relegated to the large limbo of apparently inexplicable phenomena which continually present themselves to the working pathologist.

Occasionally I found small tufts of a fungus springing from the spots, but it was doubtful whether this was not a saprophyte. Sections through the spots showed, as a rule, no more than is shown in Fig. 51, i. e. a depressed area of dead and discoloured cells, but in one or two cases I found what looked suspiciously like a definite mycelium in the dead tissues, as shown in Fig. 52.

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As time went on it seemed significant that the fungus which made its appearance, when the spotted parts were kept damp for a few days under a bell-jar, always presented the same characters; but as this and other modes of culture led rather to the conclusion that the fungus was saprophytic in nature, nothing further came of the matter at the time beyond the accumulation of a few more drawings and notes—the lilies were spotted, and as with many other cases of spotting on leaves, stems, etc., I could not explain the puzzle. At the end of May and beginning of June this year (1888) the same lilies began to show unmistakable signs of ill-health: the lower leaves shrivelled and died, and leaf after leaf in succession on the flowering shoots went off. By the middle of June the plants were looking very bad indeed, and I recognised the small orange and brown spots on the (still healthy) buds in much greater numbers than ever before, and the problem arose once more—how are the spots produced?

During the wet weather at the end of June many of the buds began to develop mouldy patches, and I soon found that such patches sometimes started from the orange spots already known, or from larger buff-coloured areas—the latter especially on the very damp leaves. By July I, every plant in the bed had greyish mouldy patches on the buds, as shown in Fig. I, and several of the buds were shrivelled and dead, and it was clear that the lilies were in for a severe epidemic disease.

On July 10, I noted the following as the position of affairs. There were 258 flowering stems of *Lilium candidum* in the garden, and more than 1200 flower-buds on them. Half of these buds were already ruined, and less than 10 per cent. were presentable: in fact the vast majority were in the condition exhibited in Fig. 1. Every leaf on the lower parts of the plants was decayed long before, and nearly all the small upper leaves and bracts were spotted and blotched like those in Fig. 1.

By means of marked specimens, around the eight pedicels

of which I tied coloured worsted, the following facts were elicited as to the progress of the disease.

A spot like that in Fig. 2 on July 10, had changed to the condition shown in Fig. 3 on the 16th, and the whole bud was black-brown and rotten (Fig. 4) on July 24. Another bud had three very minute spots on July 8, and on the 19th the bud was beginning to open, the spots having altered little, if at all; on July 24, this bud opened, and its outer perianth-leaves showed several dirty buff spots; otherwise the flower was a good one. And similarly with others. The normal course of events was that a spot, like that in Fig. 2, enlarged till it became like that in Fig. 3, usually coalescing with others on the same bud, until sooner or later the bud was entirely blackened and shrivelled as in Fig. 4.

The same course was observed in other organs, especially in the leaves. In all cases it was noticed during the wet weather that a rich growth of a grey mould-like fungus made its appearance on and around the buff-coloured spots, and increased as the bud decayed (Figs. 1, 3). To my surprise, this 'mould' turned out to be, not one of the Peronosporeae or any such form known to be a virulent parasite, but a fungus of the kind often called Botrytis or Polyactis—a form I had occasionally observed in previous seasons as a presumable saprophyte, and which is usually regarded as only a saprophyte. Of course the first question to be decided was whether or no the Botrytis had really any causal connection with the spots, or whether it merely followed some other form as a scavenger living on the products of the ravages caused by it. It is true the latter seemed the most probable explanation, but there were some facts against it in the present instance, and as the sequel shows the Botrytis turned out to be a parasite, at any rate in this particular case. Before describing the methods and results which led to this conclusion, however, I will describe the fungus as found growing on and in the lily-buds, and the phenomena presented by it when cultivated in artificial and natural nutritive solutions.

A vertical section through a badly diseased patch (Fig. 3), or through buds in the conditions shown in Figs. 1, 4, shows that the grey mouldiness is due to countless erect branched conidiophores, which burst through the cuticle of the epidermis from the tissues inside, and bear the conidia or spores (Figs. 5, 9). The conidiophores stand off from the surface into the damp air, and usually attain a height of about one to three millimeters: as will be shown later, they may attain much larger dimensions under certain conditions fulfilled in cultures. Each conidiophore bores its way through the walls and cuticle of the epidermis-cells (Figs. 7, 10), grows erect for some time, and then puts forth from two to five or more stout, short branches: meanwhile the main stalk has become septate, and its walls pale sepia-brown in colour. The conidia begin to arise as little peg-like projections from the swollen ends of the branches (Fig. 9 c), the ends of the pegs becoming enlarged and filled out more and more with protoplasm.

In such sections as Fig. 5, taken from buds already thoroughly destroyed by the fungus, the hyphae from which the conidiophores spring are found to occupy every part of the bud: not only are all the lacunae and cell-cavities of the calyx and corolla completely full of mycelium, but the tissues of the anthers and ovary likewise. Between the pollen-grains, between the ovules, and even in the tissues of the latter, are the finer hyphae of the fungus, branching in all directions. Moreover, no traces of distinct cells are to be found, for the hyphae completely occupy the substance of the cell-walls, as well as the cavities, and reduce the whole tissue to an amorphous mass of swollen, brown organic substance, in and through which the mycelium is running; so that, as seen in Fig. 5, the remnant of what was the tissues of the bud now forms a mere discoloured packing, so to speak, between the interwoven hyphae.

Sections through a bud in the state shown in Fig. 3 present a less advanced stage of destruction: the epidermis and subjacent tissues beneath the buff-coloured area are utterly

destroyed (Fig. 6), but in the green parts around there are no hyphae. From the densely packed hyphae in the epidermis, thin branches descend almost vertically through the tissues below (Figs. 6, 7), and emerge at length through the epidermis of the inside of the perianth-lobe, cross the slight interspace between this lobe (sepal) and the edges of the petals which it overlaps, and so infect the interior of the bud. As I shall have occasion to show later (though I did not know it till after infections had been artificially carried out), the spread of these hyphae is facilitated by the poisoning action of the hyphae on the tissues around them.

Sections through still younger spots, e.g. a little more advanced than Fig. 2, show that the hyphae are as yet entirely confined to the cell-walls (Figs. 55, 56), in the swollen substance of which they are growing and branching in all directions, but especially in a plane parallel to the surface of the organ.

In the neighbourhood of the mycelium, e.g. at the margin of the diseased area in Fig. 3, the cell-walls bounding the lacunae, and those of the epidermis and guard-cells of the stomata, are often found to be swollen and turning brown and granular (Fig. 8). This was a phenomenon which greatly puzzled me until I found that it is due to the action of a soluble ferment excreted by the fungus itself, and which slowly diffuses around and kills the cells.

The mycelium in the tissues is richly-branched, septate, and colourless, excepting that with age the cell-walls assume a pale sepia-tint. The branches which come to the exterior to form conidiophores are also at first colourless: as they grow older the cell-walls quickly turn brownish (Fig. 9), as also do the ripening conidia. All the parts are filled with a dense fine-grained or minutely vacuolated protoplasm, in which I have seen no definite nuclei, at any rate with ordinary staining reagents. At the same time, it should be mentioned that no special search for nuclei has been undertaken in detail.

The ripe conidium is of an ovoid form, and usually pale sepia in colour, and very large for a *Botrytis*; its average size

being about $\frac{1}{60}$ to $\frac{1}{60}$ mm. long by about $\frac{1}{70}$ to $\frac{1}{60}$ mm. broad. At the slightly narrower end may often be seen the remains of the peg-like sterigma by which it was attached to the conidiophore. As will be shown later these conidia are formed and ripen very rapidly, and they germinate at once in water at even a comparatively low temperature—e.g. 8° –10° C.—provided they have access to air. They are wetted with difficulty at first, but soon absorb water and swell, and the protoplasm is then seen to be nearly homogeneous, with minute brilliant granules here and there.

In Fig. 11 I have drawn the chief stages of germination in water at a low ordinary temperature, such as prevailed this summer. The spore was sown in a hanging drop at 11.30 a.m.: at 2.30 p.m. it had commenced to germinate, α , its protoplasm becoming frothy, and pushing the cell-wall out at two points as colourless germ-tubes. At 7 p.m. the same day, the terminal germ-tube had grown to about four times its previous length, while the second one remained as a mere protuberance on the side of the conidium and developed no further, Fig. 11 α'. Growth continued during the night, and by 10 o'clock next morning, the germ-tube was about five times as long as the spore, and had put forth a branch, and developed several septa, a''. The conidium was now almost empty, a large vacuole occupying its interior, a'', and several vacuoles were formed in the proximal segment of the germtube; otherwise the protoplasm was bright and homogeneous. No further growth occurred, however, as the supply of foodmaterial was now exhausted.

A second example is given in Fig. 12, where it will be seen that the process was quite similar, the second germinal tube attaining a somewhat greater length before ceasing to develop further: and this time it was the terminal hypha which was the weak one.

It is well worth notice how very little food-material is necessary to change the manner of germination in these water-cultures: it has happened in a drop containing two or three conidia, that one has died, and in a few hours it can be observed that the hyphae of the others are more vigorous—they have been slightly nourished by the remains of the dead spore.

If the conidia are sown in a drop of suitable culture-fluid, instead of in pure water, the influence of the food-supply makes itself felt from the first moment of germination, as is at once evident on comparing the preceding figures with Figs. 13–16, and Fig. 32.

The chief difference is that the mycelium grows more rapidly, and of course for a longer time in the nutritive solution; moreover, the germinal hyphae are from the first more numerous, and full of active, brilliant protoplasm, and branch soon and frequently. The septa are also more As before, I can describe all the numerous and close-set. chief phases by reference to a concrete example, drawn at the various stages. The spore shown in Fig. 14 was sown in a drop of Pasteur's solution, where it lay at the edge, at 7 p.m. on July 7th; at 10 a.m. on the 8th it had germinated, and put forth the four hyphae exhibited in the drawing. At 7 p.m. on the 8th, i.e. twenty-four hours after sowing, considerable changes had occurred, as shown in Fig. 15. In the first place, the hypha which took the lead in germination has grown but little, and already shows signs of exhaustion, while the two smaller hyphae have practically ceased to develop. All the energy of growth has, in fact, passed into the curved, upper hypha of Fig. 14, and this drawing was selected because it is so easily recognised through the various stages by means of the knee-like curve of the chief hypha. In Fig. 15 this hypha has grown to many times its former length, has branched considerably, and is full of protoplasm of the peculiar, brilliant, fine-grained, non-vacuolated character which distinguishes actively growing fungi. Only its basal segment is slightly vacuolated, as is also the spore. The particularly one-sided development of this young mycelium is not hard to explain: the spore lay, as said, at the margin of the drop of culture-fluid, and the fortunate hypha with the peculiar kneelike curve at its base happened to be pointing towards the

central part of the drop, and grew in the direction of abundant food-supply.

By 8.30 a.m. on July 9th, the mycelium had grown too large to be drawn under the higher power, and Fig. 16 shows its relative dimensions under a much lower objective (Zeiss B, instead of D). The chief changes noticeable are the increased branching, and the formation of certain peculiar cross-connections by the fusion of the tips of lateral hyphae, of which I shall have more to say presently. Three such cross-unions have been formed, as shown at x, and these are only the forerunners of many more, as may be seen in Fig. 17, which shows the same mycelium on July 11th, i.e. two days after the last, as far as could be sketched on one plane. As shown by the lines bounding the rectangular area depicted, there are a few leading hyphae which run out beyond the drawing; but these are not important. What is more important, however, is the development of numerous, short, erect hyphae leading up to the lower surface of the cover-slip, and certain others which go down into the depths of the damp-chamber. These hyphae, being at right angles to the general plane of the mycelium, could not be drawn in such a sketch, but I hope to make their conformation and arrangement, etc. intelligible in what follows. Even a glance at Fig. 17 shows that very numerous cross-connections are now established, so that the mycelium has become a real net-work of hyphae; it should also be noted that the general character of the mycelium has now been changed by the development of numerous tufts of thin, sinuous, tendril-like hyphae, chiefly at the ends of lateral branches. Complex as this four-days-old mycelium already is, it is not difficult to trace still the main, stouter branches of the previous stages; these give off branches in all directions, and of many degrees of tenuity. Excepting that several of the larger branches have more numerous septa than before, and that their protoplasm is now more or less vacuolated, and their walls begin to show a tinge of brown, there are no further changes of importance to be noted in Fig. 17.

We may now pass to the description of some of the details of such a normal mycelium as that exhibited in Figs. 14–17, and first may be taken the shorter branches, which run up more or less at right angles from the main mycelium to the lower surface of the cover-slip, from which the whole culture is suspended; and as I shall have a good deal to say about these peculiar branches, it will be necessary to describe them in some little detail.

The first remarkable fact about them is that they grow vertically, or nearly so, until they come directly in contact with the glass cover-slip, their tips then flatten themselves on the glass surface, and soon afterwards they are found to be sticking to the glass so tenaciously that they cannot be removed without destroying them and their branches. They are clearly the bodies which have been described by De Bary 1 as 'Haft-organen,' and I shall therefore term them organs of attachment.

Any one of these organs is developed as follows. A branch rises nearly vertically from the mycelium hanging on the lower free surface of the culture-drop, and its tip swells as it comes in contact with the cover-slip; if the culture-drop is very shallow, these club-shaped branches may meet the glass obliquely from the first.

Soon after contact the organ is seen to have a bright spot at the centre of the attached portion, as shown in Fig. 20 at x, and in Figs. 22 and 24. Round this brilliant spot the walls of the hypha, closely pressed to the glass, gradually become thicker (as seen in optical section), and acquire a faint, brownish tinge. It is then seen that the outer contour is surrounded by a glairy film, as shown in Figs. 22 and 24.

These appearances are not difficult to explain. I have drawn at Fig. 22 the tip of the organ of attachment as it would appear in profile, the double horizontal lines representing the outline of the section of the cover-slip. Viewed from above in the direction of the arrow, we should see a pale,

¹ Comp. Morph. and Biol. of Fungi, etc., Engl. ed., p. 45.

bright spot, because the light meets with least obstruction or deflection at that part; not only is the structure more translucent in that direction, but the neighbouring contents may even be acting, so to speak, as a lens. The glairy film surrounding the organ is deliquescent substance of the cell-wall, the organ being firmly attached by the conversion of part of its walls into a gum-like substance, and I shall shortly demonstrate that this must be due to the action of a ferment excreted by the tips of the hyphae when they come in contact with the glass. When contact is first made these hyphae are full of dense, bright protoplasm; in other words, the strong hyphae are very active. As the walls thicken and stick to the glass, and darken in hue, the protoplasm becomes more and more vacuolated, and may finally be nearly all used up, the changes being very much as in the case of the branches in Fig. 45. Before this, however, the attached organ may branch, at or near the extreme tip (Fig. 24), or further behind; such branching often occurs before attachment, as shown in Figs. 21-25.

It remains to be said that these organs of attachment are not necessarily confined to the vertical branches; for on older cultures, where the air in the damp chamber is kept sufficiently moist, branches growing off from the surface of the hanging drop come in contact with the sides and bottom of the chamber and form just such organs, sometimes in enormous quantities.

These organs may also be much more complex than any figured in the plates, branching repeatedly just below the apices, until, occasionally, a tassel-like tuft of close, short hyphae is formed (Fig. 26), all the tips of the short branches flattening themselves vertically on to the glass. Everything, in fact, points to these organs being of the same morphological nature as those figured by Brefeld in *Pesisa sclerotiorum*¹, and explained by De Bary subsequently as organs of attachment.

¹ Schimmelpilze, Hft. IV. Taf. ix. Figs. 11 and 15.

The next feature of interest in the mycelium is the crossconnections of the hyphae, a phenomenon of constant occurrence in cultures of three or four days old and upwards. As seen in Fig. 17 these cross-connections may be very numerous, and may occur, so far as I can make out, between hyphae of all orders. The least interesting case is when two hyphae lying nearly parallel and close together simply become joined by cross-branches, as in Fig. 19; but in the same figure I would draw attention to the remarkable case shown at x, where a branch, short and thick, coming down from the upper hypha, is met by two small and much thinner ones from the lower one. These two small thin branches have obviously bent over towards a common point, the extreme tip, of the larger branch, and then fused with it. But two other little branches have also been developed from the lower hypha, and their ends are also curving over towards the same point, as if to fuse with the large hypha.

It was such cases as this, and some still more remarkable ones which I had observed in another fungus growing on potatoes, which led me to place cultures under continuous observation, so that I could follow this process of conjugation of the hyphae. It is not necessary to describe in detail the precautions and preparations necessary for this: active cultures in hanging drops are placed beneath microscopes, certain branches are fixed in the field of view, and records made from time to time. It is simply a matter of patient observation, aided by a little experience in choosing hyphae likely to emit the conjugating branches before night.

In Fig. 27 is a case which came under notice so to speak accidentally, because I was at the time following the development of the organs of attachment, and was watching the tip of the hypha to that end.

The hypha α was drawn at 7 p.m. on July 18th. At 6.30 a.m. on the 19th it had grown slowly (the temperature being low) to the extent shown in b; c represents the state of affairs at 10 a.m. on the same day. At 11.40 a.m. on the same day (July 19th) a branch was beginning to develop as a minute

protuberance, x in d, on the lower side of the terminal segment of the main hypha, and from the first this branch was directed towards the second segment of the branch below. At 12.30 this was very distinctly seen to be the case, for the protuberance in question was curved slightly backwards, so that its apex travelled in a line at right angles to the axis of the branch below; but (as shown in e) a second protuberance was by this time apparent, springing from the middle segment of the lower branch and with its axis in the same line as that along which the apex of the first one was travelling. At 12.55 (Fig. 27, f and g) these two protuberances were nearly in contact by their apices; and by 1.10 p.m., as seen in h, they had become united, and their protoplasm continuous, the double partition where the tips came in contact having been dissolved away.

As will be seen by referring to Figs. 28, 29, and 30, very similar phenomena are observed in others of the numerous cases of these fusions of small lateral branches (Fig. 30), or of larger terminal ones (Fig. 28), and the next step is to see if any explanation can be offered of this strange process.

It seems to me, after observing numerous cases of these fusions in this and other fungi, that we must distinguish between two steps in the process. In the first place there is some cause at work which determines the formation of a branch, and then, in the second place, we have to assume that some other cause determines the direction in which the branch grows, at least in the cases given and in similar ones. now, we give due consideration to the development of the densely branched organs of attachment which have been described above, it seems suggestive that copious and rapid branching occurs at just those places where the solvent action of some substance in the protoplasm is most evident. I may anticipate matters so far as to state that it is just at these parts that a ferment capable of swelling and dissolving cellulose is formed most abundantly, and it is in the highest degree probable that the presence of this ferment determines the place of origin of the branching.

I have tried to figure the process to my own mind somewhat

as follows. The protoplasm, confined in a segment, goes on forming the ferment, until, there being no substance for the ferment to employ its energies on, the quantity of the latter becomes so great that it can no longer be retained, and the cellulose-wall undergoes softening at some point and is pressed forwards as a protuberance, a young branch. I imagine, moreover, that the continuous forward growth of the apex of any hypha takes place in a similar way, that is to say, the ferment-substance at the apex keeps the cellulose of the hypha at that place in a soft, extensible condition, and the pressure from behind stretches it and drives the tip forwards.

Next comes the second point, the direction in which the hypha or branch is constrained to grow. If we carefully examine cases such as those shown in Figs. 27 to 30, it seems to me impossible to doubt that the hyphae exert an attractive influence upon one another, just as do the zoospores of certain algae, or as the contents of archegonia have been shown to attract spermatozoids, and the filaments of Spirogyra react on one another when conjugating 1. A little reflection will show that, in principle, the cases I have here brought to light are by no means isolated ones. I may simply remind the reader that the oogonia of certain Phycomycetes not only attract the antheridial branches2, but, if De Bary's supposition be correct, even determine their formation; then, again, the neighbouring sporidia of the Ustilagineae have long been known to conjugate in pairs, the connecting tubes taking the shortest course between the two sporidia³. Such junctions as I am describing are much more common than is generally supposed, and in all the cases known to me it is difficult to avoid the impression that the two (or more) bodies concerned are attracting one another in some way. When one sees a hypha deflected from its previous course through nearly a right angle as in Fig. 28, and I have seen cases in another fungus where the deflection

¹ v. Pfeffer, Unters. d. Bot. Inst. z. Tübingen, I. H. 3.

² Beitr. zur Morph. u. Phys. d. Pilze, IV.

² See esp. Brefeld, Bot. Unters. ü. Hefenpilze, 1883; De Bary, Biol. of Fungi; also Marshall Ward, Phil. Trans., B, 1887, Pl. 12.

amounts to considerably more than a right angle, it seems to me impossible to avoid the impression that some attraction is exerted.

I have tried to account for the phenomenon of the directive action as due to heliotropism or geotropism, but entirely without success; indeed, I never met with a fungus which seemed more indifferent to light than does this one, and the direction of the branches seems to have nothing to do with the direction of gravitation. There are two factors, however, which do seem to be of importance when considering the whole question of the direction of growth and the fusions of the hyphae; these are, firstly, the contact of hyphae with one another, or with a solid substance, and secondly, the direction in which the food-material lies with regard to free hyphae. Thus, as has already been pointed out, the contact of the young organs of attachment with the surface of the cover-slip stimulates them to exude ferment-substance and to branch, and the same is the case when they come in contact with the epidermis of a leaf or bud of a lily, with the difference that the exuded ferment there causes dissolution of the tissues, and the branching takes place in the dying mass of cells. In both cases, however, we have the irritation of contact first inducing accumulation of ferment at the spot, and branching follows. That one cause of the direction of growth of free branches is the presence of food-materials is suggested by the mode of development of such mycelia as the one in Figs. 15 and 16, where the successful growth is all into the drop of culturefluid, and similar directive influences are exerted by the tissues when once infected, as may be seen by the direct plunging in of the leading hyphae in Figs. 6 and 7, for plenty of evidence exists to show that these hyphae follow paths of least resistance prepared for them by a ferment in advance. Even in a culture liquid, and much more so in these cases, it may be a fair question whether the dissolved substances do not act as irritants keeping the ferment towards the tips of the hyphae. and if so there is no essential difference between the two cases so far.

Although I believe that the branching is due to the localisation of ferment-substance in the hyphae or segment, and that the nutritive medium may have an influence in directing a growing branch when once formed, it seems quite clear that this gives no explanation whatever of the remarkable phenomenon of the attraction which leads to the junctions between the hyphae; and in the numerous cases, like those figured in Figs. 27-30, I cannot bring myself to believe that these factors alone determine the course and fusion of the Moreover, I have convinced myself that mere hyphae. contact between hyphae does not necessarily involve fusion, for in the case figured in Fig. 31 the upper hypha, having come accidentally in contact with the lower one, is seen to slide over in contact with the latter, without fusing with it at all, suggesting that one or both of the hyphae need to be in some special condition—I assume they must contain the ferment-substance in some necessary quantity or condition of action, or both-before they can conjugate. It is true that junctions are often established later in such cases as Fig. 31, at the point of contact where the two hyphae cross one another; but this only tends to prove the accuracy of the surmise that at the time of contact there was no attraction and no fusion, but that continued irritation at the point of accidental contact slowly causes a local accumulation of the ferment, and fusion eventually results at that point. It might be remarked that the case last quoted reminds one of the behaviour of some Myxamoebae prior to fusion into a plasmodium 1, for in this instance also we are compelled to assume that some remarkable state is necessary before fusion can occur.

It remains to raise at least two more questions concerning this phenomenon In the first place, how is the attraction to be regarded? and in the second place, what object is served by the conjugation? To these questions I can give no definite

¹ See Marshall Ward, An Aquatic Myxomycete, in Studies from the Biol, Lab. of the Owens College, vol. i, 1886, Pl. III and IV, pp. 64-85.

answer, and perhaps it is scarcely worth while to speculate further on so obscure a problem; but it might be a fair subject for inquiry whether the action of the exuding ferment on the medium, i.e. food-materials in solution, is not to render the latter more directly available, and so mark out a track of least resistance as it were: at the same time it is not easy to see how this could happen in a liquid. It might also be asked whether the object served by the fusions is to nourish the whole mycelium more equably, or to equilibrate certain differences which have unavoidably made themselves apparent in the metabolic processes. In any case, the question at bottom seems to be a wide one, and possibly one affecting the particular case of reproduction in general. I do not suggest that this is a reproductive process as usually understood, but it seems probable that the stimuli concerned are fundamentally of the same nature.

We may now pass on to consider further cultures of the *Botrytis*, and the development of its conidia and conidiophores under conditions which could be controlled.

I have cultivated it as a saprophyte in the following media in addition to the normal Pasteur's solution, viz. in Pasteur's solution which had been partially exhausted by growing a crop of the fungus on it, and then filtered and sterilised; in Pasteur's solution to which various proportions of peptone were added; in cold water-extract of crushed bulbs of *Lilium candidum*; in cold water-extract of raisins; and in certain other media which will be described subsequently, such as distilled water with bits of lily-bulb, fruit-juices neutralised with alkalies, and so forth.

In all these media the spores germinate, but the free development of the mycelium only continues when the liquid is acid, and the degree of acidity may be considerable. In a distinctly alkaline liquid no germination or growth whatever took place.

In all cases the course of development was the same in general, but with differences in detail. Confining attention for the present to the cultures in hanging drops, I found that

in small drops of thin solutions, or in drops of partially exhausted Pasteur's solution, the mycelium produced fewer and poorer organs of attachment, and soon proceeded to the development of the conidiophores, and then ceased to grow further unless new food-materials were added; in denser and richer solutions, or in larger drops, on the contrary, the mycelium often grew from 10–12 days without passing to the development of the conidiophores. In the former cases it was possible to trace the whole development of the conidiophores and conidia without difficulty, because, there being few obscuring hyphae, etc., the same specimen could be kept under constant supervision.

In Fig. 32 I have drawn a mycelium cultivated from a single spore in a drop of partially exhausted Pasteur's solution: the culture was five days old. As seen, the mycelium is not very large or complex, and even the original spore can be recognised at S. On the hyphae at various places are large numbers of bubbles of gas, A A, a common occurrence when conidiophores are about to be produced: such bubbles are also found on the conidiophores themselves (Fig. 35) so long as they are submerged, but as they usually project from the surface of the drop of culture-liquid into the damp air of the chamber, the gas-bubbles are often not seen on them.

At CC in Fig. 32 are several conidiophores, bearing the well-known heads of *Botrytis*-spores which look like bunches of grapes. The conidiophores are produced in centrifugal order, by the outgrowth of thick blunt hyphae (Fig. 39) from certain not well defined branches of the mycelium.

The development is best illustrated by describing a concrete case—Fig. 34. The outgrowing colourless hypha is very full of dense protoplasm, often delicately vacuolated, and its rather blunt end soon begins to swell into a club-like shape: in this condition it looks very like the young sporophore of *Mucor*, only it soon becomes septate at short intervals. In the case figured this stage was reached by 4.45 p.m., and beneath the club-like end of the branch two little protuberances were appearing (Fig. 34, 1). At 5 p.m. the protuberances had grown out into

club-like arms, 2, and at 5.30 they, as well as the terminal swelling, were apparently studded with minute colourless spikules, 3, which grew in length but did not increase in number. Fig. 34, 4, shows their condition at 5.45. Each of these spikules is a minute peg-like branch from the club, the protoplasm of both being continuous. At 6.5 p.m. (the same evening throughout) the little pegs or *sterigmata* were beginning to swell at their ends into minute, clear, bead-like bodies, 5, which were well defined at 6.15, No. 6, as young conidia, the rapid completion of which is most extraordinary—7 being drawn at 6.25, and 8 at 6.40 p.m.

Up to this stage the conidiophore may be still colourless, but after some hours of ripening, the sepia-hue shown in Fig. 9 makes its appearance. As already stated, these conidia fall from the sterigmata and germinate at once; they may even begin to germinate in some cases while still attached to the sterigmata.

It has sometimes happened that a young conidiophore becomes encrusted with minute crystalline particles (Fig. 36) which may be oxalate of lime: in my cultures, however, this has not occurred to any great extent except in those where raisin-extract was used.

One more feature needs description before we leave the conidiophores. In cases where the food-material is abundant, the conidiophore forms, as a rule, several successive heads of conidia in the following way. When the first head of conidia has been completed, a lateral branch springs from beneath the next septum lower down, as shown at x in Fig. 33, and this branch elongates considerably, becomes septate, and in its turn forms a terminal head of spores (Fig. 37), and this process may be repeated several times 1 (Fig. 38): in a strong culture, in fact, I have had each of the branches in such a case as that of Fig. 38 bear eight successive tufts of spores, one new one being developed every 12-14 hours.

¹ The resemblance of these forms to Corda's *Gonatobotrys* is obvious. The same process occurs in the conidiophores of *Sclerotinia Fuckeliana*. See De Bary, Biol. of Fungi, p. 48.

It will be seen from the foregoing how very rapidly the conidia develop when once they begin to form. I have a few other observations on the rate of growth of the ordinary hyphae, but they are not sufficiently extensive or systematic to be of much value: they are added here simply to show how measurements might be made if the subject was pursued.

Thus, the young conidiophore in Fig. 39 was growing at the apex at such a rate that the portion x-x' in a increased to x-x' in b, in the interval between 11.30 a.m. and 3.20 p.m. (the temperature averaging $12^{\circ}-15^{\circ}$ C.), and two more septa were put in.

As another instance I may refer to Fig. 40, where the mycelium was growing in a culture-drop in which a piece of lily-bulb was suspended. At 2.55 p.m. a hypha was seen in the position shown in the drawing (Fig. 40 a): b shows the relative positions at 3.5 p.m., and c at 3.30 p.m., the temperature averaging $12^{\circ}-1.5^{\circ}$ C.

In Fig. 41, the hypha a was in the position drawn at 3.2 p.m., its apex pointing towards an intercellular space of a piece of lily-bulb near it. At 3.7 p.m. its tip was at the first x, and at 3.12 it was at the second x; the temperature was as before. As already stated, I regard these as mere notes taken by the way, since I was not at the time concerned with the question of the rate of growth, being in fact engaged in observing the entrance of the hyphae into pieces of tissue: so far as they go they are accurate, but numerous observations would be needed to make the matter clear in all its details, and it is not improbable that this fungus would afford a very favourable object for such observations.

I now pass on to the consideration of a phenomenon which seems to be of considerable importance, and so far as I can discover has never been described before.

In cultures of the fungus, both in hanging drops and on a larger scale, it is often noticed that the tips of the hyphae, at a certain stage of development, exude small drops of a translucent viscous fluid or semi-fluid substance, containing a number of minute brilliant granules; these drops may then enlarge and become distinctly granular, at the same time gradually acquiring a yellowish or slightly brownish hue (Figs. 43–45). I had occasionally seen a similar exudation of drops in previous cultures of fungi, and found among my drawings of cultures made in Ceylon in 1880 several similar cases; so far, however, I had not been able to establish any satisfactory explanation of the phenomenon, though the idea arose that the drops might be due to some substance manufactured in the cell in larger quantity than could be retained. Before offering a more definite explanation, I will describe the drops and their exudation in detail.

If the slightly swollen ends of vigorous hyphae of a well nourished mycelium be watched, it will be seen that sooner or later some of them become very full of particularly brilliant protoplasm (Fig. 45, 1); if such a hypha comes in contact with a solid body, such as the cover-slip, it simply begins to cling to it, and branches to form an organ of attachment as described on p. 327. If it remains free, however, it gradually begins to exude a small translucent or nearly transparent viscid drop (Fig. 45, 2) from the tip, the protoplasm in the hypha becoming most beautifully vacuolated meanwhile. During the next few hours the exudation continues, and the vacuolation increases (Fig. 45, 3 and 4), and the drop slowly changes character as described-it becomes granular, and acquires a pale brownish-yellow hue. In some cases the segment of hypha becomes nearly emptied and collapses, and I at one time suspected that the whole matter was merely a case of over-turgidity due to the absorption of water in quantity too great for the elasticity of the cellwalls. But it soon became evident that even if this were the case, there must be some cause at work determining the absorption of water at just that period in development. But when one reflects that these drops are extruded from vigorous hyphae developed in Pasteur's solution, or in the juices of fruits, etc., which can by no means be regarded as calculated to cause vacuolation by physical action, but, on the contrary, would act physically rather as plasmolysing agents,

then it seems clear that we are here concerned with a process depending on changes in the metabolism of the plant—the hyphae, under the conditions given, extrude drops of substance from their tips. What is this substance?

On examining the margins of large mycelia (from one to four or five inches in diameter) grown on the surface of Pasteur's solution in properly sterilised flasks, I have found nearly every hypha extruding these drops (Fig. 44), and it was not difficult to obtain definite reactions. The drops react to Millon's test by giving a very evident and characteristic brick-red colour; nitric acid followed by ammonic hydrate results in the well-known golden yellow of the xantho-proteic reaction; Schulze's solution colours them yellow to yellow-brown, as also does iodine alone; alcohol coagulates them, and they stain with such dyes as would be expected to colour proteids.

All this, of course, would point to the drop consisting simply of the extruded protoplasm of the cell, and it will no doubt be asked why I regard it as anything else.

For the two following reasons, I look upon these drops as consisting in great part of a soluble ferment which has the property of swelling and dissolving cellulose cell-walls; I am not prepared to affirm that the drops in my cultures consist solely and entirely of the ferment, for it is far more probable that mucilage and proteids are mixed with it, and that the ferment only constitutes the brilliant colourless granules which become dissolved out from the extruded mixture of the drops. The two reasons upon which I lay such stress are, (1) I have succeeded in observing under the microscope the tips of the hyphae actually penetrate into and through the cellulose cell-walls of thin sections of lily-bulb placed in their path; and (2) a watery extract of the mass of hyphae referred to is found to swell up cellulose cell-walls when thin sections are placed in drops of it. Much of the rest of the present paper is concerned with the elucidation of these noteworthy phenomena.

But first, to make one or two further remarks concerning

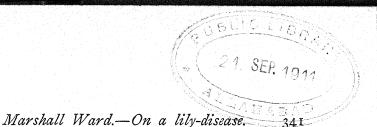
the 'ferment-drops,' as they may be termed. They occur in cultures growing in extract of raisins, etc., as well as in Pasteur's solution, and so far as I can determine, their formation depends not so much on the medium in which the fungus is growing as on the stage of development the plant has reached. So long as the mycelium is rapidly extending, i.e. developing numerous lateral branches, many of which are conjugating in the manner described on p. 329, the extrusion of the drops is not observable. When a stage approaching maturity is reached, however, and rapid growth is ceasing, then the tips of free hyphae, and of the branches of organs of attachment, may be seen to extrude the drops.

If a mycelium in this condition is placed upon the epidermis of a young lily-bud, the branches attack the tissues very actively, and destruction follows rapidly, and I may quote this as a further reason for believing that the drops contain the ferment. If to a mycelium in the condition above described, fresh food is offered, e.g. by adding a small drop of the culture-fluid, then active growth and branching etc. recommence, and the extrusion of the drops ceases meanwhile.

I think these facts point to the probability that so long as active growth and increase of surface of the fungus are going on, the ferment is not accumulated in undue quantities at any particular place, and no doubt the cross-connections established by the conjugating hyphae (p. 329) still further insure its distribution: as soon as this distributing process is brought nearly to a standstill, however, the ferment still being prepared by the protoplasm accumulates in quantities greater than can be retained, and breaks through the cellulose-walls in the manner described.

I may add that there is nothing absurd in supposing that ferment is still being formed after active growth has ceased, for such a preparation of ferment is regarded as taking place in the tubers, bulbs, etc. of higher plants during their periods of rest¹, and, further, the fact of the solution of the cell-walls

¹ Cf. Sachs, Lectures on Physiology, p. 352.



in contact during the conjugation of the hyphae of the cross-connections may be cited as evidence that the ferment can dissolve its own cell-walls; moreover, the deliquescence of the walls of the organs of attachment (p. 328) points to the same conclusion, as also do known phenomena in other fungi.

We may now pass to the description of cultures and methods by which I succeeded in observing the actual piercing of the cell-walls by the tips of the hyphae of this fungus, and then to the subject of the action of aqueous extracts of the mycelium on cellulose, since these are the two important points to establish in proof of the above conclusions. Having found that when slices of the buds or leaves of the lily were placed in the culture-drop in which a spore was germinating, it was very difficult to avoid the introduction of foreign organisms, and that even when bacteria did not spoil the culture the products of disorganisation of the chlorophyll-corpuscles, etc. obscured the observation, it became necessary to adopt some modification of the process: this was successfully accomplished by the following means.

In the first place I employed glass-slips and covers which had been heated to near redness in a porcelain evaporating dish, and made the damp chambers of newly sterilised bibulous paper: then, taking care that none of the apparatus was touched with anything but recently heated forceps, needles, and freshly drawn glass capillary tubes, I placed a small drop of distilled water in the centre of the cover-slip¹ by means of a freshly drawn capillary pipette, and sowed one spore in the drop. The single spore was obtained as follows. The conidiophores under a damp bell-jar usually have a tiny dew-drop at their ends, in which are numerous conidia, and it is not difficult to lift this off clean, with the point of a sterilised needle; the drop with its contained conidia is then placed in a larger drop of pure water, and the drop then fished with a clean needle. The needle lifts a small drop,

¹ This is not so easy to do as it may seem, for the surface of the perfectly cleaned glass is often so readily wetted, that the drop is apt to spread as a film.

which is placed on the cover-slip and examined with the microscope: if it only contains one spore, it is selected—if it contains more than one, the whole is rejected, and a new cover-slip and drop taken, and so on. Having obtained a satisfactory drop of water with one spore, I then placed in the drop also a thin section of either the ovary from a young lily-bud, or of the central scales of a lily-bulb, cut with a perfectly clean razor. Such sections may be cut quite clean and free from foreign spores, etc., if care is taken in removing the outer coverings, and I found that such sections of the bulb shaken up in freshly distilled water to remove some of the starch-grains could be kept clean in the cultures for more than a week.

The most interesting results were obtained from such cultures. The pieces of bulb yielded to the water sufficient nutriment to start the germinating fungus-spore, and a normal mycelium was generally obtained on the third day.

In such cultures I have over and over again traced the hyphae growing across the field until their tips reach the piece of bulb, and observed that as growth proceeds the thin cellulose-walls of the bulb become swollen and evidently softened. I have also over and over again watched the tips of the hyphae enter into the substance of the cellulose-walls. and continue their growth in the plane of what would be the 'middle lamella' if such could be distinguished in these very thin walls. Moreover, such hyphae occasionally bore through from cell to cell, as shown in Figs. 57 and 58, thus placing beyond all cavil the significance of these observations. describe a concrete case:—In Fig. 58 the hypha was observed to gradually approach the edge of the section of lily-bulb, and to come vertically in contact with the cell-wall, figured at a, at 2.55 p.m.; the onward growth of the hypha continued, pressing the tip against the surface of the wall and deflecting it slightly, as seen in b, c, and d. The progress of this mechanical effect was quite visible at intervals of two or three minutes, and in fact b was drawn at 2.58 p.m.; c at 3.0 p.m.; and d at 3.2 p.m., which of course implies that the changes

were going on quite as rapidly as I could sketch them. attaining the condition represented at d (Fig. 57), however, the effect of the irritation on the tip of the hypha began to make itself apparent; the tip slowly sank into the substance of the cell-wall (e was drawn at 3.7 p.m.), and appeared as if it was becoming continuous with its substance. This process went on for a quarter of an hour (f was drawn at 3.15 p.m.), until, at 3.24 p.m., the tip of the hypha, like a tiny bright globule, appeared, g, on the other side of the cell-wall: this rapidly enlarged, like a yeast-bud, and in four minutes presented the appearance shown in h(3.28 p.m.) and rapidly elongated to a continuation of the hypha (i was drawn at 3.30 p.m.). The hypha had pierced the cell-wall, slightly obliquely, by means of its tip. Now the tip of this hypha was just such an one as I found to extrude what I have called the 'ferment drops,' and it seems to me perfectly safe to assume that in this case the ferment at the tip was used to soften the cell-wall of the lily-bulb.

It should be remarked that in this case also the fungus is living as a saprophyte: the tissues of a section such as I have described are dead after a few hours at most of the treatment to which they have been subjected. I remind the reader of this, simply to show that it is not claimed for these observations that they demonstrate exactly what goes on when the fungus is living as a parasite. That they bear directly on that question is of course obvious enough. I need say no more about Fig. 57 than to observe that it illustrates a similar case of the rapid piercing of a cell-wall, the condition b being attained ten minutes after a.

As already said, it is much oftener the case that when the tip of the hypha enters the cell-wall it runs in the plane of the middle lamella between the cells: I have not added figures of this, since what refers to Figs. 54-56 sufficiently illustrates the results of these cultures also.

It remains to state that the hyphae do not directly attack the starch-grains, nuclei, or other cell-contents, though they affect them indirectly: the starch-grains, for instance, are sometimes found to stain with methyl-violet after the action of the fungus on the tissues for two or three days.

I have in my possession, and can show, excellent permanent preparations of such cultures as have been described, and it may not be superfluous to describe briefly how such preparations may be put up.

Owing to the circumstances of the formation of the organs of attachment, it is always comparatively easy to secure any culture of more than three days old, and if the cover-slip with its hanging drop is lifted with forceps, and placed gently on the surface of a vessel of hardening reagent, on which it floats with the culture downwards, it usually happens that the mycelium, etc. is hardened with little or no disturbance. After many trials, with all kinds of stains, etc., I find that picronigrosin gives by far the most satisfactory results: after 24 hours the most delicate mycelia are beautifully fixed and stained, and the hardening may be then completed in absolute alcohol. After two or three changes, at intervals of a day, the alcohol has removed all the picric acid, but the specimen is stained steel-blue in various shades, and is so thoroughly hardened, that it may be passed through oil of cloves and xylol, and finally mounted in canada balsam, without collapse. When I state that I have thus mounted mycelia, showing the extruded 'ferment-drops' fixed and stained, it will readily be seen that the process is as satisfactory as it is delicate. I have also thus fixed and mounted cultures such as those described on p. 354, showing the hyphae in situ in the substance of the cell-walls (Figs. 55, 56).

If picric acid alone is used, the hardening may be accomplished similarly, and the preparations (after being washed with absolute alcohol) stained with carmine, methyl-violet, aniline blue, etc.; after careful and prolonged washing to remove every trace of acid, beautiful haematoxylin preparations may also be made. Such specimens may be so well prepared as to preserve the vacuolation in the hyphae: I have not been satisfied that nuclei exist in the hyphae. Some of the dyes bring out very clearly the zone of mucilage round the organs

of attachment, and, as already stated, some of the methylviolet preparations of cultures with bulb-sections show the starch-grains deeply stained violet.

I have also obtained very beautiful results by thus hardening and staining whole buds of the lily in various stages of disease, and it may be remarked that this method of hardening and staining, especially with methyl-violet, affords a very easy test for the presence of fungus-hyphae or -spores on the epidermis of a leaf; and any one who is ignorant of the prevalence of fungi on leaves of all kinds during such a summer as the past one, may easily convince himself by laying the decolourised and hardened leaf in methyl-violet, and then examining the outside of the epidermis—the hyphae stand out sharp and clear on the colourless background. I have used this method with great success in infections, picking out spores and germinal hyphae with startling clearness: the method was also of the greatest use in preparing sections of the diseased tissues, such as those shown in Figs. 6, 7, 55, 56, etc.

Another very satisfactory method is to place the hardened and stained mycelium, attached to its cover-slip, in absolute alcohol which is floating on a layer of pure glycerine. In the course of a few days, the preparation with its cover-slip sinks into the glycerine, and may be removed and mounted in glycerine-jelly, the superabundant glycerine being gently washed off after the glycerine-jelly is thoroughly hardened. I also possess some very delicate preparations mounted in glycerine only.

In preparing some of these mycelia, and especially when placing pieces of large cultures — mycelia 3–4 inches in diameter, and obtained in a manner to be described below—directly into absolute alcohol, it was usually noticeable that a white, apparently crystalline deposit fell to the bottom of the watch-glass or other vessel. I had the strongest reasons for believing that this precipitate carried down with it the ferment referred to so often, though I had not as yet obtained the precipitate in sufficient quantities to make positive statements concerning the white powder itself. Of this more will be said presently.

I now pass to the consideration of the second of the two statements on p. 339, viz. that aqueous extracts of the mycelium contain a ferment which swells and dissolves cellulose.

On reflection it seemed probable that if the 'ferment-drops' really contained the ferment, then, since the hyphae exuded the drops into the Pasteur's solution and other liquid media, one ought to be able to detect it there by its action on the tissues¹; in other words, if the extruded drops contain a ferment which dissolves cellulose, then the liquid containing the ferment ought to have a solvent action on cellulose.

My first experiment met with decided success, so far as it went, for on placing thin sections of the bud of a lily in a few drops of the Pasteur's solution in which the fungus had been growing for several days, they underwent a distinct alteration in the course of the night, whereas similar sections in the same liquid, treated similarly except that it was boiled for two minutes, underwent no such change. The alteration consisted in a decided swelling and softening of the cellulose of the cell-walls, rendering their stratification remarkably distinct, and causing them to refract the light in a peculiar manner (see Figs. 59 and 60).

Since I could not be sure that such a solution was, so to speak, quite clean, or entirely devoid of other organisms, it became necessary to start a series of pure cultures on a larger scale to see if the phenomenon was a constant one.

After trying several methods, I finally adopted the following one as giving the best results on the whole. Flasks of about half a litre capacity were selected, washed, and heated on a sand-bath; when cool, they were carefully charged with about a quarter of a litre of the solution to be used—Pasteur's solution, with or without peptone, sterilised cold-water extracts of raisins, lily-bulb, etc.—and at once placed on a sand-bath, and the liquid boiled for 10–15 minutes; the neck was stopped

¹ A ferment which causes the swelling and alteration of cellulose was found by De Bary in *Peziza Sclerotiorum* (Bot. Zeit. 1886, Nos. 22-27), of which more shortly, and by Beyerinck in the Gumming of Trees under the influence of *Coryneum Beyerinckii* (Archives Néerlandaises, T. xix (1884), p. 43).

with cotton-wool after five minutes' boiling, and while steam was rushing out. Next day the boiling was repeated for ten minutes; and after yet another twenty-four hours the boiling was again repeated, and so on. This well-known process of discontinuous sterilising gives excellent results.

In charging the flasks with spores I abandoned the method of sowing with the point of a heated needle, because it was not possible by this means to get any idea of the number of spores taken up, and still less of the purity of the sowing. The following modification of the ordinary process gave satisfactory results.

Perfectly clean sowings were made in drops of the sterilised culture-fluid on small cover-slips which had been heated until nearly red-hot, as if for culture in hanging drops; Ineed not give details as to the precautions taken, but of course the cover-slips were not touched after sterilisation except by heated forceps, needles, glass, etc. The sowings, as made, were examined under the microscope, the cover-slip resting on sterilised glass or metal rings, so that the drop hung from its lower surface. When I was satisfied by microscopic examination that the sowing was clean -i.e. contained only the Botrytis-conidia—the cover-slip was lifted by forceps at one corner, the cotton-wool plug removed for a moment from the neck of the flask, and the sowing and cover-slip dropped bodily into the culture-liquid in the flask; then the plug was replaced and pushed well in, and the flask labelled and placed on a shelf, where it remained perfectly still at a suitable temperature.

In the course of three days the tiny mycelia can be seen on the surface of the liquid in such flasks, and in less than a week it is usually possible to decide whether after all care a foreign spore has obtruded (as will happen occasionally) in the culture. In a fortnight the mycelia have coalesced, and cover the liquid as a grey sheet: further growth results in corrugation or folding of this sheet as it tries to extend in the confined space.

None of the hyphae dip far into the liquid, nor do the aërial hyphae project far from the surface; at the margins,

organs of attachment are developed in contact with the glass, and conidia are formed on the surface of the sheet, but not in large numbers or in big heads, probably owing to the restricted access of free air.

With such cultures as these the following series of experiments were instituted.

SERIES I.

On July 17, three flasks were prepared and sterilised, corked with cotton wool, etc. as follows, and conidia of the *Botrytis* sown in them.

I = Pasteur's solution.

2 = Pasteur's solution, and a little peptone.

3 = Fresh urine.

On August 1, dense mycelial crusts had formed on Nos. 1, 2, corrugated and growing out in all directions.

On No. 3, a mere film had commenced to form, and had then perished.

I then (August 1) filtered 1 the yellow liquid of No. 1 into two test-tubes, which had been properly sterilised: these tubes may be called A and B respectively.

I then boiled the liquor in A for two minutes: that in B was left untouched.

Damp chambers, properly sterilised, were then prepared as for cultures in hanging drops, and used as follows:—

- a =Two were arranged with the hanging drop of the boiled liquor (test tube A) and a thin section of lily-bulb-scale placed in the drops.
- β = Two others were arranged exactly as above, but the drops consisted of the unboiled liquor (test-tube B).
- γ = Two were arranged as in a (i. e. the drops consisted of boiled liquor), and two spores of the *Botrytis* placed in the drop as well as the lily-bulb-section.
- δ = Two others were arranged exactly as in γ , but with drops of the unboiled liquor.

¹ Not without considerable difficulty.

On August 1, at 6 p.m., these damp-chambers were placed in a larger moist chamber in the laboratory, the temperature being 12°-15° C.

On Aug. 2, at 10 a.m., I examined the above with the microscope.

The sections in α and γ were practically unaltered, but those in β and δ presented a curious appearance, due to the peculiar brilliance of their cell-walls: the cellulose was somewhat swollen, and refracted the light so that the edges of the walls appeared coloured. It was evident that something in the liquid had caused a change in the cell-walls of such a kind that they became diffluent and swollen: moreover this something was destroyed by boiling.

I also devised the following parallel arrangements, as a sort of check on the foregoing.

On Aug. 1, eight culture-chambers were prepared as before, and the hanging drops constituted as follows:—

- ϵ = Two of distilled water only.
- $\zeta =$ Two of Pasteur's solution.
- $\eta={
 m Two}$ of distilled water, with one or two Botrytisspores in.
- $\theta = \text{Two of Pasteur's solution with one or two } \textit{Botrytis-spores.}$

These eight cultures were placed in a similar dampchamber to the preceding eight, and at the same time; and they also were examined when the preceding ones were.

So far as the cell-walls were concerned, i.e. neglecting plasmolysis and other easily explained alterations, the sections in these cultures showed no change. The spores germinated normally.

I was by no means satisfied with these experiments; for although there was a distinct swelling of the cell-walls in the cases marked β and δ , it was not quite so conspicuous as in my rough experiment described on p. 346. However, repetition of the observations again led to the conclusion that the cell-walls did undergo the changes described.

On Aug. 2, I took the remainder of the Pasteur's liquid from flask No. 1, and employed it in three parts.

Part I was gently decanted into a clean test-tube: the nearly clear liquor contained a few spores and bits of mycelium.

Part II was filtered with difficulty into a second test-tube, yielding a clear yellowish liquor as in previous cases.

Part III was not only filtered, but also boiled for five minutes.

The tubes were stopped with cotton-wool, and marked X, Y, and Z respectively, and in each tube I placed one or two short bits, with smooth clean-cut ends, of the bud, leaf, peduncle, and bulb of the white lily.

The tubes were then left until 10 a.m. on Aug. 4—i.e. about 40 hours—in an ordinary temperature. The changes which had then ensued in the test-tubes X and Y were sufficiently obvious to be seen with the unaided eye, especially with the short cylindrical bits of peduncle.

Whereas those in the tube Z (boiled liquor) still preserved their sharp smooth-cut ends and edges, those in X and Y (and especially in X) had their ends swollen and gelatinised, and projecting both longitudinally and laterally over the cut epidermis, so that the pieces looked like dumb-bells, the handle being formed of the intact epidermis and cuticle compressing the tissues beneath, and the heads of the swollen cells radiating at the ends.

Sections and microscopical examination showed that the tissues of the pieces in the test-tube Z were practically unaltered; in X and Y, however, the 'heads' of the dumb-bell-like pieces were composed of the separated swollen cells of the cortex and pith. Something in the liquor had in fact caused the dissolution of the middle lamella and the gelification of the cellulose. That this something is a ferment is not only highly probable from the preceding, but becomes almost a certainty from the case with which it is destroyed on boiling the liquor. There were no bacteria to be observed in the fluid.

Having repeated these experiments with like success, it seemed probable that better results, i.e. more intense action, might be got by employing an aqueous extract of the fungus: with this object the following series of experiments were made.

SERIES II.

On August 4, I removed with a newly drawn glass hook the mycelium from a flask-culture of three weeks' standing: the mycelium was about 4 inches in diameter, and about 3 mm. thick, grey in colour, and of a tough almost cartilaginous texture. This mycelium was then crushed in a mortar in its own juice, i.e. with so much of the liquor as it had carried away from the flask, and a little distilled water. Owing to its slippery, semi-cartilaginous character, it was not easily pounded: after the operation the unpleasant-looking mess evolved a distinct sickly smell, not evident before crushing.

The whole mess was then poured into a clean flask, and the neck stopped with cotton-wool, and allowed to brew for an hour.

The liquor was then poured off and divided into two equal parts, as follows:—

Half was filtered into a small test-tube, labelled, and left intact.

The other half was filtered into a second tube, and boiled for five minutes.

The results were similar to those obtained previously; slices of lily-tissues placed in the unboiled liquor had their cell-walls swollen, whereas those in the boiled liquor underwent no such change. Again, however, I felt that the amount of swelling of the cell-walls was too slight to be absolutely convincing, so the following method was tried.

¹ The process of filtering was difficult: for the first minute or so the liquor came through fairly rapidly, but it afterwards filtered through very slowly indeed. Thinking this might be due to some action on the filter-paper, I examined the latter subsequently; but I was unable to satisfy myself that the fibres were altered.

SERIES III.

A fine mycelium, about the same size as the last, was removed on August 7th from its flask (it had been growing since July 17th on Pasteur's solution with a little peptone), allowed to drain, and pounded as before in a mortar, but with the addition of a few cubic centimetres of distilled water, instead of its own juice. The pounded mass was allowed to stand for an hour at the ordinary temperature, and then three sets of culture-chambers were arranged as in Series I.

In the first set of three chambers, the hanging drop was of the raw unfiltered extract.

In the second set, also of three chambers, the drop was of the unboiled but filtered liquor.

In the third set, also of three, the drop was of the boiled and filtered extract.

In each drop was placed a thin section of the peduncle of the white lily, and the preparations were examined from hour to hour.

In sets one and two the results were observable in the course of the first hour, and after six hours the cellulose-walls were all striated and swollen as in Fig. 60. It should be remarked that the swelling action was more vigorous in the unfiltered liquor than in the filtered one.

In the third set, where the drop consisted of the filtered liquor boiled for five minutes, no swelling of the cell-walls was observable in six hours.

I now felt satisfied that the action was really due to a soluble ferment, of the nature of a zymase, excreted by the fungus in question; but the question still remained as to the possibility of really isolating the ferment, for it had to be admitted that such an extract as the above must contain a mixture of substances.

Adopting the well-known method of precipitation by alcohol, the following experiments were carried out.

SERIES IV.

A six-weeks' culture of the *Botrytis*, on Pasteur's solution with a little peptone, was removed from its flask, and the thick fungus-crust pounded in a mortar with a little distilled water: the mess was then allowed to digest for a few hours at 28°-30° C. It was then filtered, the filtered liquor falling into a tall tube, and four or five times its bulk of alcohol was added. Contact with the alcohol at once caused a milkiness, which rapidly increased on agitation; and in less than a minute a series of flocculent white masses formed throughout the liquid, some of which slowly sank to the bottom, others floated quietly to the top. The tube was left to stand all night, at the ordinary temperature, and in the morning the white bulky flocks had increased a little, and numerous small tufts of a like nature were sticking to the sides of the tube.

I removed some of the floating flocculent masses, and examined them with the microscope: they consisted partly of amorphous substance reminding one of fibrine, and partly of crystalline substance of at least two kinds. I thought at first that the crystals might possibly be those of tyrosin chiefly, with some leucine, but that idea was not supported by their examination by a chemical friend. Be this as it may (and it is of secondary importance because the crystals etc. only act as a vehicle), the partly amorphous, partly crystalline flocks, after being dried at the ordinary temperature over sulphuric acid in the partially exhausted receiver of an air-pump, formed a greyish mass, which swelled and partly dissolved in distilled water.

I placed some of it in a small watch-glass, with a little distilled water, and allowed it to digest two hours; I then added a few sections of the pedicel of *Lilium auratum* (being unable to obtain *Lilium candidum*), and allowed them to soak for eight hours at 30° C. The results were as before—the middle lamellae of all the parenchyma cells were destroyed, and the cells isolated as if they had been boiled, while the cellulose-

walls swelled up, and became distinctly lamellated and folded as in Fig. 6o.

Similar sections, lying for an equal time in the boiled solution, gave no such reactions, nor did sections lying in water.

It seems clear, then that the precipitated flocks carried with them a substance which dissolves in water and produces the changes in cellulose which have been described; and I think it will not be denied that this substance is the ferment so often referred to. As yet, however, I cannot claim to have isolated the ferment in a state of absolute purity, though it seems probable that this will yet be accomplished. It seems extremely probable that the ferment is of the same nature as the one extracted by De Bary from carrots which were destroyed by the mycelium of *Peziza Selerotiorum*.

Having now obtained a fairly complete history of the *Botrytis* as a saprophyte, we will proceed to describe its behaviour as a parasitic fungus. As will have been seen from the previous part of the paper, I was led to attempt infections on account of the peculiar behaviour of the small spots on the leaves and buds, etc.

During July and August conidia were several times sown in drops of distilled water, on the surface of young lily-buds, or of leaves, obtained from non-infected plants at a distance as well as from specimens nearer the infected area.

The conidia germinated readily on the epidermis, and in from 20 to 48 hours the germ-tubes were usually found in the solid cellulose-substance of the cell-walls of the epidermis. Looked at from above, as in Figs. 46 and 47, it was by no means obvious at first that the germ-hyphae had penetrated the cuticle; but closer observation showed that the tips of the longer or shorter germ-hyphae attached themselves to the surface of the cuticle, and then dissolved their way in, discolouring and destroying the cell-walls and cuticle in the immediate neighbourhood. In no case did I see the end of a germ-hypha enter a stoma, though it is by no means denied as improbable that such an entrance may occur. It was often

possible to assure myself that the protoplasm of the conidium passed into the germ-hypha in the cell-wall, and the hypha branched and grew in the plane of the surface of the bud, leaf, etc. Moreover, transverse sections through the recent infections show beyond all doubt the presence of the hyphae in the substance of the cell-wall, as seen in Figs. 55 and 56: these preparations also show clearly that the cellulose in which the hyphae are running is swollen considerably, and it seems impossible to reject the explanation that this is due to the action of the ferment secreted by the fungus, and isolated by precipitation, as described, and that the change here is of the same nature as the swelling of the cellulose in the experiments referred to on pp. 348–353.

Among other variations of the conditions of infection, I tried the effect of sowing the conidia in drops of Pasteur's solution on the epidermis of the buds and leaves. The phenomena of infection were not markedly different, the chief noteworthy point being that the germ-hyphae gave rise to branches outside as well as inside the cuticle. These outside hyphae then repeatedly branch, and form organs of attachment which rapidly destroy the cuticle beneath, and enter the tissues: such a case is illustrated in Fig. 50, the specimen being observed from within. This exceptional mode of infection is peculiarly interesting, because it resembles one described by De Bary¹ as the only mode occurring with the mycelium derived from ascospores of Sclerotinia (Peziza) Sclerotiorum, where the mycelium is incapable of becoming parasitic unless it has previously been nourished as a saprophyte. Here, again, as will be shown later, the entrance of the hyphae into the tissues depends upon the excretion of a ferment which dissolves cellulose. I shall, however, return to this point subsequently.

But perhaps the best and most convincing preparation showing the causal relation between the fungus and the spots was the one figured in Fig. 53. I had several times found that

¹ Bot. Zeit. 1886, Nos. 22-27.

a mycelium exists in the dead cell-walls of the red or brown spots, such as that of Fig. 2, and among numerous sections I found the one drawn (Fig. 53). In order to make out more details it was allowed to swell slowly in very dilute ammoniasolution, and the spore then came into view, its germ-hypha having entered beneath the cuticle, and grown and branched in, and at the expense of the gelatinised cell-walls, which were in a collapsed state when the section was cut.

Such preparations as this and those in Figs. 51 and 52 leave little doubt that what takes place in infection is as follows. The *Botrytis*-conidium germinates on the damp epidermis, and the tip of the germ-hypha excretes sufficient of the ferment to soften and dissolve the cell-wall, which it then penetrates. Feeding on the substance of the dissolved and swollen cellulose, the hyphae grow and branch more and more, and excrete larger and larger quantities of ferment. The cells thus attacked lose water, and the protoplasm dies and turns brown, and finally the whole may collapse, and leave simply a shrivelled mass of brown dead cells, in the dried-up walls of which the young mycelium is trapped, and may persist in a dormant condition. In this way are produced the discoloured sunken spots so characteristic of the disease in a certain stage.

If there is sufficient water present to ensure that the swollen cell-walls do not dry up, then the hyphae branch and grow in the cellulose as shown in Figs. 55 and 56, and soon gain sufficient energy to put forth numerous branches downwards and in all directions, destroying the subjacent tissues with extraordinary rapidity (as in Figs. 6 and 7). That the mycelium in the small, brown, sunken spots is only in a dormant condition can be shown by keeping these under a damp bell-jar; it is only because the cell-walls have dried up too rapidly that the mycelium lies in a dormant condition, because the ferment cannot diffuse and prepare the path of destruction necessary for the rapid progress of the hyphae, the growth of which is of course also dependent on the presence of water.

I may now consider the very difficult and involved question

of the nomenclature and systematic position of this fungus. It will have been noted that it has been referred to in this paper throughout, so far, simply as a *Botrytis*, and it should be added that I have used this term in a broad sense: it may now be useful to see if this sense can be narrowed.

The genus Botrytis was first introduced by Micheli, but gradually became so split up and altered, that its original signification was practically lost. It used to include the group Peronosporeae, until Corda separated Peronospora, and De Bary showed that the so-called Botrytis infestans of the potato-disease must not only be separated as one of the Peronosporeae, but must be placed in a distinct genus among these, and he re-named it Phytophthora infestans. The old genus Botrytis also contained a number of other forms which have since been separated under various names. Thus Link removed Haplaria, a form common on waterplants; and he divided many of the remaining forms into Botrytis proper and Polyactis. Allied to these, and variously arranged with them among the so-called Mucedines, were the forms Gonatobotrys, Botryosporium, etc. 1

All such arrangements were based almost entirely on the description and figure of observers who took the forms as they occurred at the moment of observation, paying little or no regard to the possible changes they might undergo in the course of their life-histories. The classical case of *Peronospora* (*Phytophthora*) infestans may be quoted as showing the results to be obtained by patient and careful study of the details of development. When De Bary and others had elucidated the biology of the potato-disease fungus, it was seen

¹ See Berkeley's Cryptogamic Botany, and Cooke's Handbook. Polyactis is again united with Botrytis (as a sub-genus) by Saccardo in his 'Sylloge' (vol. iv. p. 116), the group thus containing about 100 'species.' The genus Botrytis is defined by him as follows:—'Botrytis, Mich. em. Link.—Hyphae steriles repentes; fertiles vage dendroideo-ramosae, erectae. Ramuli modo tenues apice acutiusculi (Eubotrytis), modo crassiores obtusiusculi (Polyactis), modo apice inflato-verruculosi (Phymatotrichum), modo apice cristulati (Cristularia). Conidia prope apicem ramulorum varie congregatae nec vere capitata, continua, globosa, ellipsoidea v. oblonga, hyalina v. laete colorata.'

that its only claim to alliance with its supposed congeners lay in a superficial resemblance during one phase of its life-history. Now, apart from other instances, it has resulted from the studies of Tulasne (who first demonstrated that Botrytis (Polyactis) cinerea is the gonidial form of a Discomycete), Brefeld, De Bary, and others of the school of mycologists who have striven to found species and genera only on a knowledge of the entire life-history of the forms, that the group of forms known as Polyactis among English authors, but still called Botrytis by the Germans, are really only stages—gonidial or conidial forms—in the life-history of certain Pezizas¹.

The question now arises, to which, if any, of these groups is the fungus of this lily-disease to be relegated. It is not a question to be answered off-hand, in face of the warnings to be gathered from a consideration of the many mistakes which have arisen from authors founding species on incomplete information; nor do the descriptions of authors help us much, though good figures exist in some cases and are of great service in the process.

But there is other evidence to hand, which has to be discussed, for the disease in question, together with its fungus, has been already noticed in England, and in part described. On referring to the 'Gardeners' Chronicle,' for 18812, there is a short article on the subject by the Rev. M. J. Berkeley, beginning with remarks on a letter from Mr. Wolley Dod. In this letter we are informed that various species of *Lilium*, and especially *L. auratum*, after a fortnight or so of wet, stormy weather, had become spotted—'Rust-coloured patches come upon the leaves of buds as if they had been burnt; if the buds are not completely destroyed, the flowers become imperfect and distorted; and the whole plant has a blighted appearance.' All kinds of lilies were attacked in the beds in

¹ Thus, as has so often occurred with Fungi, different phases in the life-history of one and the same form have received special names. Cf. De Bary, Biol. of Fungi, p. 238.

² P. 340.

the open, but specimens in pots under the shelter of green-houses escaped. Berkeley, who seems to have been already acquainted with this disease, points out that it is due to the ravages of a fungus presumably allied to *Peronospora*, although he had never seen it produce zoospores.

Berkeley named this fungus Ovularia elliptica¹, and says the spores are 'elliptic, resembling in shape and size those of many of the larger Pezizas.' As we shall see, there was probably something approaching the prophetic in this intuitive remark. The disease received no further notice, so far as I can discover, until the past summer. In the 'Gardeners' Chronicle' for August 18th, 18882, Mr. W. G. Smith gives a good outline figure of the conidiophores and conidia of this fungus, and—on evidence of the slenderest possible nature alters the name of the fungus to Peronospora elliptica. I feel no difficulty in concluding that the fungus is the same in all cases, though of course it is barely possible, or rather conceivable, that two different forms have been mixed up. However, Mr. Smith's drawing suggests that the fungus is a 'Polyactis,' and the suggestion receives support if we turn to his own capital figure of Polyactis vulgaris (Botrytis vulgaris) in the 'Gardeners' Chronicle' for Febuary, 18863, where this fungus is described as following other fungi on and in diseased Cucurbitaceae.

Now it so happens that this *Polyactis vulgaris* has been very abundant on the vegetable marrows in my garden this year (in August and September), and I have taken considerable pains to cultivate it from the conidia in the pure condition. I have also cultivated with equal ease and care a similar, if not identical form of *Polyactis* on *Phaseolus*, also in my own garden.

These cultures have shown that the conidia, sown in Pasteur's solution, rapidly give rise to a mycelium of branched, septate hyphae, which form cross-connections, organs of attachment, and in short behave almost exactly as the conidia and mycelium of the fungus of the lily-disease. I cannot

^{1 &#}x27;Floccis hie illic nodosis, sporis magnis ellipticis laevibus.'

² p. 184.

yet positively assert that the *Polyactis* on *Phascolus* is the same as that on the marrow, but the differences, if they exist, are so slight as to escape detection.

But although *Polyactis vulgaris* behaves so far almost exactly like the lily-fungus, there are one or two points of difference to be noted, of sufficient importance to prevent any one from confounding them; to make myself quite certain of this, I made simultaneous sowings of the three forms—that on the lily, that on *Phascolus*, and that on the vegetable marrow—in drops of the same brew of Pasteur's solution, and all treated exactly alike.

In the first place, the conidia of the lily-fungus are about twice as large as those of the *Polyactis* 1 on beans and marrows;

¹ It is neither necessary nor useful to give a full list, but the following data are of importance in the discussion which follows:—

Polyactis vulgaris, Fr., has conidia measuring $10-12 \times 7-9 \mu$, according to Saccardo. If we take the measurements of different observers, however, the conidia must vary considerably, from $10-16 \times 7-10 \mu$.

Polyactis cana, Berk., has spores measuring 30-33×15-18 μ, as I learn from Mr. Massee, who has kindly examined the specimens in Berkeley's Herbarium at Kew for me.

Polyactis cinerea, Pers. (Botrytis cinerea of the continental writers), has conidia measuring $8-9 \times 6-7 \mu$, according to Saccardo.

Polyactis fascicularis, Corda. The conidia measure 12-15 × 6-8 μ.

Now these are the chief British forms in Cooke's Handbook (1871, vol. ii. p. 601), *Polyactis vera* being a rare form of which I have no measurements.

Mr. Massee has been so good as to send me drawings and measurements of the following additional forms: I have also to thank Mr. G. Murray for measurements of several species:—

Polyactis capitata, Berkeley's Herb., a white form with conidia measuring 20-25 × 12-16 μ.

Polyactis umbellata, DC., a dark rusty-brown form with rounded conidia measuring $15^{-17} \mu$.

And a very interesting form *Botrytis (Cristatella) corolligenium*, Cke. and Mass., found at Kew on decaying *Calcoolaria*-flowers. The plant is pure white, and the type in the Kew Herbarium has ovoid conidia measuring $25 \times 15^{-18} \mu$.

It is sufficiently clear from the above that the lily-Betrytis, with conidia measuring about $25~\mu$ long × $15~\mu$ broad, cannot be confounded with the forms P. vulgaris or P. cinerea, or any of the small-spored forms. Nor can I identify it with Berkeley's P. cana, though his P. capitata (conidia $20-25\times12-16$) seems to present some not unimportant features of resemblance. This could only be decided by comparing fresh specimens and by cultivation. In any case, it seems clear that, if there is anything at all in the measurements, we must look for this 'species' among the large-spored forms.

secondly, the spores of the latter germ inate more rapidly, and at once—much more quickly than those of lily-fungus—proceed to the development of large organs of attachment of the complex tassel-shape, like those in Fig. 26.

Some time ago I received from Kew a piece of moribund stem of an Amorphophallus, covered with a grey mould which turned out to be a Botrytis (Polyactis), very like P. vulgaris, if not identical with it: in the interior of the stem were numerous small black sclerotia, each about the size of a piece of mouse-dung, and exactly resembling it to the unaided eye. These sclerotia arose from the same mycelium as the Botrytis, and cultures of the conidia of the latter gave rise to mycelia, etc., exactly similar to those just described for Polyactis vulgaris. I mention this because it affords another indication of the kind of fungi we are here concerned with, and furnishes another confirmation, if one is needed, of the connection between Botrytis (Polyactis) and the sclerotium-bearing Pezizas.

But there is abundance of evidence in addition to show that the fungus of the lily-disease is a *Botrytis*, of the *Polyactis* group, from which I may select the following.

In 1877-78 Eidam¹ published some interesting results. He cultivated the spores of *Botrytis elegans*, Lk., in nutritive solutions such as extract of plums, and obtained sclerotia developed from the mycelium.

In 1880 Frank² published an interesting account of a fungus parasitic on turnips, the mycelium of which developed both sclerotia and *Botrytis*-conidia: the sclerotia produced a *Pesiza* which Frank calls *P. sclerotioides*, Lib., but, as De Bary³ points out, this is a slip for *P. Sclerotiorum*, Lib. Frank also calls his *Botrytis*, *B. cinerea*, a name which De Bary rejects, because *B. cinerea* is the *Botrytis*-form of *Pesiza Fuckeliana*. Be this as it may, Frank found that the conidia of his *Botrytis*, when sown in the turnip-plant, put forth germ-hyphae

¹ Ber. d. Schles. Gesellsch. 1878, p. 151. Bot. Zeit., 1878, p. 174.

² Die Krankheiten der Pflanzen, p. 530.

³ Bot. Zeit., 1886, p. 457.

which directly infected it, and produced a mycelium which developed sclerotia, and again *Botrytis*.

In 1886 Sorauer 1 published the result of his investigations on a disease of onions, caused by a *Pezisa*. Here, again, he found that a *Botrytis* was developed as well as a sclerotium, and that infections could be made with the *Botrytis*-spores.

That Botrytis cinerea is only a conidial form of the sclerotium-bearing Pesisa Fuckeliana has long been established, as already said, and an excellent account of this fungus is to be found in De Bary's book².

In 1886 De Bary published a remarkable paper 3 on 'Some Sclerotiniae and Sclerotium-diseases, in which the attempt is made to clear up much of the obscurity which hangs around this group of Pezizas. In this paper De Bary gives in detail the results of his study of Pesisa Sclerotiorum, Libert 4. He assumes a knowledge of the structure and development of the black sclerotia and the long-stalked funnel or trumpetlike hymenophores (the *Pezisa*-form), giving some facts of importance for their identity. The trumpet-like form is especially characteristic of the clay-coloured cups. spores are discharged by ejaculation from the asci, and may thus be obtained very clean and in any quantity. Each spore is ellipsoid, measuring on the average about $11-12 \mu$ long by $4.5-6 \mu$ broad. De Bary expressly states that no gonidiaform of this fungus is known, and all his cultures were from the ascospores.

The ascospore germinates at once in culture solutions,

¹ Handb. der Pflanzenkrankheiten, ii. p. 294.

² Comp. Morph. and Biol. of Fungi, etc., 1887, Engl. ed., especially pp. 219, 224, 380.

³ Bot. Zeit., 1886, Nos. 22-27.

⁴ Sclerotinia Libertiana, Fuckel. This Periza is named Hymenoscypha Sclerotiorum, Lib. in Phillip's British Discomycetes, 1887, and has received many other names.

⁵ The best general account of the sclerotium is in De Bary's Morph, and Biol. of Fungi, pp. 218, 219, etc., and in Brefeld's Schimmelpilze, iv. p. 112; also Pirotta, N. Giorn. Bot. Ital. xiii. p. 130. Other references are given in the first-mentioned book.

developing a mycelium of branched, septate hyphae, which form cross-connections, and develop organs of attachment so like those already referred to that no one can doubt their being organs of the same kind: they are of the tasselform so rare in the lily-fungus, however, and more like those formed by the *Botrytis* on *Phaseolus* and vegetable marrow, than those of the lily-fungus. After forming numerous organs of attachment, the *Peziza*-mycelium, if well nourished, proceeds to develop sclerotia on the surface, and in centrifugal order.

De Bary then goes on to show that his *Peziza* can be cultivated with ease as a saprophyte on many kinds of pabulum—wine-must, juices of fruits, and artificial solutions,—and that its ordinary mode of life is saprophytic; but that under certain conditions it becomes a parasite, and the most remarkable point in his paper is the demonstration of how this facultative parasitism comes about.

As a parasite, it may attack (1) reservoirs of reservematerials, especially carrots and turnips; (2) the seedlings of various dicotyledons; and (3) the vegetative parts of older dicotyledonous plants. He expressly states that in spite of all attempts he could not cultivate it, or find it parasitic on living monocotyledons.

It was particularly easy to cultivate the *Peziza* on carrots and turnips, the mycelium forming dense masses on the surface and in the tissues, softening them as if they had been boiled, and ending in the development of sclerotia. In the stems of living plants, the mycelium affects especially the pith and cortex, also softening the tissues, and forming sclerotia. The hyphae grow especially between the cells, destroying the middle lamella and causing the cellulose-walls to gelatinise as if boiled.

But although the mycelium of Sclerotinia (Peziza) Sclerotiorum can thus behave as a parasite, De Bary obtained the astonishing result that the germ-hyphae from the ascospores cannot directly penetrate into the living plant, and that this inability to enter living tissues persists until the young mycelium has been invigorated by nutrition as a saprophyte. In other

words, the germ-hyphae from the ascospores of this *Pesiza* are unable to pierce the living tissues, but when they have been nourished in a saprophytic manner by absorbing food-materials derived from dead organic sources, the mycelium at length obtains the power of piercing the plant and killing it.

De Bary gives several striking proofs of this, the simplest being that when the ascospores were sown on the cut surfaces of two carrots, one of which had been killed by boiling, the other still living, the germinal tubes at once entered the dead carrot and formed mycelia, sclerotia, etc., whereas they were unable to enter the living carrot at all.

The seedlings of *Petunia violacea* were found to be very sensitive to the fungus, but if ascospores were brought into a drop of water with the living seedling, the germ-tubes failed to enter the tissues of the *Petunia* for days: if both were placed in a drop of culture-solution (instead of pure water), however, the germ-hyphae of the *Peziza* rapidly grew to mycelia which at once entered and destroyed the tissues of the *Petunia*-seedlings.

Numerous other experiments led to the conclusion that *Sclerotinia* (*Peziza*) *Sclerotiorum* is a saprophytic fungus, the mycelium of which can become parasitic, however, if previously invigorated by being nourished as a saprophyte.

It is neither possible nor necessary to devote attention to all the interesting morphological points about this fungus, and the reader is referred to De Bary's paper for many details passed over here.

De Bary then goes on to show that when the mycelium has been nourished up to the necessary degree as a saprophyte, it develops the organs of attachment already referred to; these organs on coming in contact with the tissues of a plant, kill the subjacent epidermis, etc., and, flourishing at the expense of the products of solution of the poisoned tissues, gather more strength, and send down branched hyphae in all directions.

The action of these hyphae on the tissues is worth noticing. The cells in their neighbourhood are found to lose water.

and collapse, the protoplasm shrinking and turning brown; and these destructive processes extend in advance of the hyphae.

From all the facts De Bary concluded that the organs of attachment excrete a substance which poisons the cells; the latter then collapse, and their expressed sap then serves as food for the mycelium, which thereupon sends branches further into the tissues, the whole process becoming more and more active pari passu.

Having concluded that a diffusible substance is excreted by the fungus, De Bary then examined the juices expressed from his rotted carrots; and he found that pieces of the internodes of the bean, or of fresh carrot, or of seedlings of *Brassica*, if put into this juice, underwent strongly marked destruction in a few hours. This destruction consisted in plasmolysis of the cells; followed by a slight swelling of the cellulose-walls, and finally the dissolution of the middle lamellae.

To make a long story short, De Bary found that the expressed sap of the carrot, after destruction by the *Peziza*, contained a substance or substances which swell cell-walls and kill the tissues. From various experiments, and from the fact that the sap loses these properties on being boiled, it is concluded that the sap contains one or more ferments or enzymes, which cause the changes in question. This was still more clearly proved by using the fluid expressed from the sclerotia: this fluid was strongly active in dissolving the cell-walls.

Then follow experiments on a large scale to prove that the infection takes place from plant to plant by means of creeping mycelia, which produce organs of attachment on contact with the epidermis, and these act in the way described.

De Bary then points out that this *Peziza* attacks kidney-beans, Petunias, Zinnias, sunflowers, and some other Compositæ, carrots, turnips, and occasionally potatoes.

The parasitism is very remarkable; while one of two species closely allied will resist attack, plants of very distant alliances will suffer. Moreover there are some curious cases of local and individual predisposition to attack, which are discussed.

On the whole, seedling-plants suffer most, and De Bary comes to the conclusion that it is the amount of water in the cells and cell-walls which probably determines whether the plant resists or succumbs to the attack of the fungus: this, again, possibly depends on the conditions of the cellulose. As already stated, he found it impossible to infect monocotyledons.

I have quoted the substance of this paper at some length, because it seems to me to throw considerable light on the nature of the lily-fungus¹.

It is clear that in the development of septa, cross-connections, and organs of attachment, the mycelium developed from the conidia of the lily-Botrytis presents some remarkable analogies with the mycelium developed from the ascospores of Sclerotinia (Pesisa) Sclerotiorum. In its saprophytic habit, moreover, and the ease with which it can be grown on very different media, the lily-Botrytis resembles the Pesisa: in its parasitism it is more pronounced, but even here it presents some resemblances worth noting, especially in its mode of destroying the tissues of the host, by means of a soluble ferment. Here, however, the resemblances cease. De Bary expressly points out that his fungus has no gonidial stage; it could not be cultivated on monocotyledons; and it is prone to the rapid development of sclerotia. The mode of infections is quite different, and the lily-Botrytis easily forms gonidia in cultures.

Nevertheless, I am driven to conclude that, although I have never yet succeeded in growing sclerotia or peziza-cups from the *Botrytis*, it is either a stage in the life-history of a *Pesiza* of some kind, or at least its alliance lies in this direction; and, in support of this opinion, I would again insist upon the facts, already quoted, that *Botrytis cinerca* is known to be a gonidial form of *Pesiza Fuckeliana*; and several other forms of *Botrytis* are stages in the life-history of sclerotium-bearing Pezizas, though De Bary does not seem to allow the latter statement. There are many species, good and bad, of these Pezizas, and it

As I write, Dr. C. von Tubeuf, of Munich, sends me an account of a *Botrytis* parasitic on *Abies Douglasii*; the conidia measure 9μ by 6μ (Beitr. zur Kenntniss d. Baumkrankheiten, 1888, p. 4).

is only necessary to take up any systematic work on the group¹ to see what confusion prevails as to their nomenclature and classification. De Bary has shown that *Peziza Sclerotiorum* has probably received a different name for almost every species of host-plant on which it has been found, and it is in the highest degree probable that various species, good and bad, now pass under different names in England and on the Continent.

In conclusion, then, the lily-Botrytis is probably a gonidial stage in the life-history of some Peziza; whether the alternative form is developed on some other plant, or whether it is lost, cannot be said. It is quite conceivable, however, that in consequence of their pronounced parasitism this fungus and Phytophthora infestans may have lost their alternative form.

The attempt may now be made to give a general account of the disease, and to see how far we can explain the epidemic nature of this year's attack, from what is known so far.

It is quite certain, at the outset, that the fungus itself was present in the lily-beds in my garden in 1886 and 1887: why then did it remain sporadic during those years, and become epidemic in 1888? I think the explanation is to be sought along the following lines.

The parasitism of the fungus depends, as we have seen, in the first place on its power to excrete a ferment which softens cell-walls, and enables the hyphae to feed on their substance: this ferment acts best in a slightly acid medium, and it requires water, if for no other purpose, to enable the ferment to diffuse, but also because the more watery the cellulose the more easily it is dissolved.

Now if we compare the meteorological records for 1887 and 1888², especially for June, July, and August, the period of active development of the flower-axes of the lilies, it will be found that, in the district referred to, the summer of 1887 was particularly hot and dry, and the lilies that year produced

¹ E. g. Phillips' monograph (British Discomycetes) in the International Scientific Series (1887), which, by-the-bye, contains no reference to *Botrytis* or gonidial forms that I can discover.

² See Table and remarks in Appendix on page 370.

magnificent flowers. The sunshine was intense, and the general temperature high; this means rapid transpiration and energetic assimilation, processes by which hard, thick cellulose-walls are produced. The cuticle is also well developed, thick, clean, and continuous under such conditions; and growth is steady, there being no superabundance of water, the light being bright.

During the corresponding period of the past summer, however, the conditions were very different. The weather was for weeks very wet, and cold, and dull; this means a lowering of the rate of transpiration, and an increase of water in the plant; assimilation is also less energetic, and thin, watery, ill-developed cellulose-walls are one result. I had abundant opportunities of convincing myself that the young lilv-buds were gorged with water for hours at a time, and, in fact, many of them showed irregular protuberances of tissue due to the disturbances of growth consequent on this. In this dull, wet weather, moreover, respiration was going on more rapidly (in proportion to assimiliation) than is normally the case, and an increase, however slight, of the acids in the tissues may very well have resulted from this. Although the temperature was low, the turgid condition of the buds would be one cause of the thin and imperfect cuticle that often existed, and it seems not improbable that in the continued wet weather, small quantities of food-materials and acids in solution would diffuse to the outside. I made several attempts to determine this, but was unable to satisfy myself further than that the damp cuticle gave an acid reaction.

But even if the liquid bathing the cuticle contained no food-materials, the other conditions were obviously in favour of the fungus, and I have no doubt the epidemic nature of the disease this year depended, not so much on any changed properties of the fungus, as in alterations in the tissues of the host. Of course, once started, the fungus found another advantage in being able to develop such enormous quantities of conidia in the damp atmosphere, and these would be blown about in millions by the wind.

Accepting De Bary's results with Peziza Sclerotiorum, I

regard his fungus as a form physiologically midway between the ordinary saprophytic Pezizas, and my parasitic one; in other words, De Bary's fungus is in process of being educated to parasitic habits. It might be supposed at some future time to gradually produce a little more ferment in its ripening spores, or a stronger form of the ferment; if it did so it would be able to penetrate the plant at once, as does the lily-fungus, without previous invigoration by dead nutritive materials. This is, of course, a hypothesis; but I venture to point out that it is in accordance with some of our recent knowledge. and that, if clearly kept balanced in the mind as a suggestive hypothesis, it would be well worth while to work through the group of sclerotium-forming Pezizas, to see if they are not a series of fungi in the transition state of saprophytes which are gradually becoming parasites. There are some facts, indeed, which render it not improbable that this hypothesis might be extended to other groups of Pezizas, but the above is sufficient for the present. At a future time I hope to have something to say on the possible bearing of this on an old suggestion of my own as to the gradual loss of sexual organs in these fungi; for these sclerotium-bearing forms are gradually losing the last traces of them.

APPENDIX.

I add the following summary of the average meteorological record for the months of June, July, and August of 1886, 1887, and 1888, which I owe to the kindness of my colleague, Prof. McLeod, F.R.S., who has for many years tabulated the results obtained from observations at the Royal Indian Engineering College, Cooper's Hill, and which observations are communicated to the Meteorological Office every month. It is to be deplored that the Cooper's Hill Station is not provided with continuous recording instruments, and that we have no register of the amount of sunshine; nevertheless much information can be gained from the tables, from which extracts are appended.

Rain. (Inches.)		(819.)	1.382	(689.)	1.289	(615.)	2.320	(318)	1.842	(-255)	.813	(1.062)	5.954	(.191)	615	(068.)	1.765	(£86.)	2.411
Terrestrial Radiation. Minimum.		(29.0)	41.333	(30.2)	41.973	(30.4)	43.607	(35.1)	46.100	(9.18)	221.54	(36.2)	47.442	(34.1)	46.187	(9.87)	45.065	(32.3)	44.745
Solar Radiation. Maximum.		(136.1)	122.377	(134.8)	116.397	(133.8)	113.837	(140.8)	126.368	(2.681)	127.303	(+.621)	111 168	(8.421)	125.822	(6.981)	123.521	(6.981)	114.003
Temperature.	Minimum.	(38.2)	48.527	(43.3)	50.047	(++.+)	49.557	(45.3)	53.445	(+,++)	\$4.048	(41.7)	908.13	(413)	53.245	(44.3)	52,235	(42.6)	50.055
	Maximum.	(74.1)	64.436	(81.2)	69.283	(83.0)	289.49	(82.8)	182.04	(86.3)	75.042	(6.89)	63.719	(85.8)	+93.69	(80.0)	72.100	(Srs)	908.29
Pressure of Vapour. (Inches.)		.3432	0168.	.3954	4120	.3774	9968.	.4312	9+2+.	.4368	.4403	.3912	6804.	.4469	1624.	2968.	.4058	.4154	.4232
Dew Point.		48.417	51.730	22.307	53.387	50.743	52.043	54.619	54.542	54.648	22.607	51.848	\$3.194	55.626	816.29	52.377	52.830	53.393	54.003
Thermometer.	Wet Bulb.	52.477	20.99	55.896	59.520	53.827	26.803	58.252	60.345	29.865	63.013	54.555	56.223	58.155	62.257	26.200	020.09	6.010	58.300
	Dry Bulb.	56.953	62.417	621.09	67.513	57.270	62.623	62.597	67.823	66.055	73.035	192.29	-29.432) 60.842	901.19	209.89	61.593	69.626	58.966	63.573
Barometer. (Inches.)		30.0052	1226.62	30.2134	30.1834	29.9508	29.9256	29.9426	29.9178	30.0642	30.0287	29.7898	29.7825	30.0105	1086.62	30.0078	29.9728	30.0372	30.0085
		9881) amnr	382) mme	8881	Jume (9881	~ \(\text{fmf} \)	\ \ 7881) uly	SSSI	July () 9881	Yug.	1887	Aug.	{ sss1	Aug.

If now we examine this table, it will be seen that it bears out generally the truth of my personal observations on the weather of the months named in 1888, as compared with 1887 and 1886.

In the first place the barometric pressure was lower in June and July of 1888 than in the same months of 1886 and 1887, though this is not quite the case in August.

On looking at the wet and dry-bulb thermometer, we notice that in 1888 the readings of the dry-bulb were low in June, and markedly so in July and August, as compared with the corresponding months in 1886-7. As regards the wet-bulb, the same fact comes out—the readings are low. The dew-point is also relatively low; but whereas the dew-point throughout shows considerable similarity, the differences of temperature as indicated by the dry-bulb are, as said, very great.

The temperature columns are again instructive, especially as contrasted with 1887, both minima and maxima being distinctly low, for July and August especially. The same with solar radiation, a rough measure of the quantity of heat and light derived from the sun, not only are the maxima lower in 1888, but the averages are markedly so.

I have also made out some further details from the daily tables. In June 1888 the maximum temperature was below 60° F. on seven days, whereas in 1887 this only occurred twice, and in 1886 five times. In July 1888 it was below 60° F. on five days, on none in 1887, and on one only in 1886. In August this was the case on four days in 1888, but never the case in 1887 or 1886.

When we come to the rain-fall, the generalisation is strikingly illustrated, especially in July. Moreover, I have satisfied myself that this holds in detail, taking day by day. In June 1886, for instance, there were 14 days on which rain fell (including four days when the rainfall was less than '009 in., and one day on which more than 0.5 in. fell). In the same month in 1887, rain fell on eight days (including four days with less than '009 in., and one with more than 0.5 in.); and in 1888 there were twenty-two rainy days in June (including

six with a fall of less than .cog in., and one when it exceeded o.5 in.

Taking the month of July. In 1886 rain fell on fourteen days (including four with less than .009 in., and none with so much as 0.5 in.). In 1887 there were eleven days on which rain fell (including two days when the fall was less than .009 in.—on none did it reach 0.5 in.). Whereas in July, 1888, we had twenty-eight rainy days (only three of which registered so little as .009 in., while on five of them the fall exceeded 0.5 in.),

Then again in August, there were twenty-four days in 1886 when rain was registered (but sixteen of these yielded less than .009 in., and none so much as 0.5 in.). In 1887 there were twelve rainy days (including four with less than .009 in., and one with more than 0.5 in.). But in August, 1888, we had twenty-two rainy days (and only seven of these showed so little as 0.009 in., while on two days more than 0.5 in. fell). It has not seemed worth while for the present purpose to give further details than those above, but I may say that the daily register quite bears out these results.

It is a well-known fact that the estimation of the relative amounts of sunshine and cloud, blue sky, haze, etc., is a very difficult matter; nevertheless some indication of the state of affairs seems to be obtained by comparing the details for the months and years given.

I have made out that in June of 1886, 1887, and 1888, respectively, the total amount of cloud observed (two observations daily) was as follows, 600 being the possible maximum—i.e. if the sky had been completely overcast at every observation, the amount would have been registered as 600.

In June 1886 the amount of cloud=450, and there were twenty-seven days on which blue sky was registered as seen during some part of the day.

In June 1887 the cloud=376, blue sky being registered for twenty-three out of the thirty days.

In June 1888 the number recording cloud rose to 578, and blue sky was registered for sixteen days only out of the thirty.

Taking the register for July, we find 448 of cloud (out of a possible 620) in 1886, and blue sky was seen on twenty-eight of the thirty-one days.

In 1887=375 of cloud, and blue sky was seen on thirty days out of the possible thirty-one.

In 1888 the cloud amounts to 557, and only eighteen days are recorded as showing any blue sky.

If we then look at August. In 1886, the total cloud registered=413 out of 620, and blue sky was visible on twentynine of the thirty-one days.

In 1887 the cloud=399, and blue sky was seen on twenty-eight days.

In 1888 the cloud=499, and twenty-five days out of the thirty-one showed some blue sky.

Of course these are rough estimates, but so far as they go they entirely support the impression I had formed independently—viz. that the summer of 1888 has been dull, wet and cold, compared with 1887 especially.

SUMMARY.

In the foregoing memoir, I have attempted to bring out the whole life-history of the fungus causing the disease described, so far as it occurs on the living and dying lilies. Commencing with the description of the external symptoms, disease-spots, etc., I then show that the fungus always found in their tissues is a *Botrytis* (of the form now called *Polyactis*). The spores, cultivated in suitable media, give rise, after germinating in a characteristic manner, to a copiously branched and septate mycelium, with well-marked and easily-recognised morphological features, and which presents some physiological phenomena of much interest and importance.

Some of its branches form cross-connections by a process so like conjugation, that it is difficult to avoid applying that term to it; their conjugation is preceded by an attraction for one another, which is shown by mutual deflections of the growing hyphae. Certain of the free branches develop into the curious 'organs of attachment,' which glue themselves to solid bodies in much the same way as the tendrils of Ampelopsis, and develop in response to a similar irritability to contact. These organs, as well as the tips of other hyphae, secrete relatively large quantities of a ferment, and I have shown that in culture-media this cellulose-dissolving ferment may accumulate to such an extent that the hyphae can no longer contain it, and it causes dissolution of the cellulose at the tips of the hyphae, and consequent extrusion of the protoplasm and ferment in the form of drops. The details of accumulation of the ferment, so far as they could be traced by the microscope, are given, as also some interesting reactions, methods of staining, preparation, etc.

The development of the *Botrytis*-heads, or sporophores, and conidia, is given in detail, as well as some observations on the rate of growth of the hyphae. Then follow some observations of considerable interest on the passage of the hyphae in and through the cellulose cell-walls of the lily. By means of special cultures it was found possible to observe, step by step, the actual piercing of the cellulose by the tip of the fungus-hypha, and its further growth in the walls; it results from these observations that the tip of the hypha in contact with the cellulose, probably in consequence of the irritation of contact, excretes relatively large quantities of ferment-substance and dissolves its way into the cell-wall, swelling up the cellulose and feeding upon the products of solution, and causing destruction of the tissues by isolating the different cells as if they had been boiled.

I have also obtained from large pure cultures of the fungus in sterilised flasks, solutions which produce the same swelling and dissolution of the cellulose as those met with in chamber-cultures, containing sections of the peduncle, leaf, ovary, etc. of the lily, and their cell-walls and middle lamellae undergo solution in a few hours when placed in these aqueous extracts of the fungus. Since the swelling etc. does not occur if the extract is previously boiled for from two to five minutes, the

evidence is all but conclusive that the changes are due to the ferment referred to. Considerable success was obtained towards obtaining the ferment pure, by precipitation from the extracts with alcohol. In conclusion of this part of the paper I describe the phenomena of infection, and the details of the parasitism of the fungus, discussing the reasons for the disease being at one time sporadic, and at another epidemic, in its attacks.

The second part of the paper is occupied with the question of nomenclature, and the systematic position of the fungus, and I have given what seem to me very strong reasons for concluding that the fungus is a so-called Botrytis of the Polyactis-type—a gonidial form of some sclerotium-bearing Peziza. Further, that while it is certainly distinct from Polyactis vulgaris, Botrytis cinerea, and other accepted forms, it may or may not be the gonidial form of a Pesiza which has been already described. This can only be decided when the sclerotia and peziza - cups are found. Its mycelium presents several resemblances in its physiology to that of Sclerotinia (Peziza) Sclerotiorum, but such important differences occur in other respects that it must be unhesitatingly kept separate. In this part of the paper the literature is given so far as it applies, and guidance to the complete literature of the whole subject indicated. In conclusion some remarks of a hypothetical nature are offered, suggesting that the Pezizas of the Sclerotinia-group and their allies are in a transition state from saprophytes to parasites, and that the form now studied is one which has succeeded in becoming a true parasite.

EXPLANATION OF FIGURES IN PLATES XX, XXI, XXII, XXIII, AND XXIV.

Illustrating Professor Marshall Ward's paper on a lily-disease.

PLATE XX.

- Fig. 1. The upper portion of a flowering raceme of *Lilium candidum*, with the buds and bracts attacked by the *Botrytis*; the ashen-grey colour on the buds is due to tufts of the conidiophores of the fungus. Natural size, drawn July 7th.
- Fig. 2. A bud with one 'disease-spot' in an early stage of development; the depressed centre of the spot is orange-brown, the margin paler, and a zone of green surrounds the whole. Nat. size.
- Fig. 3. The above spot in a later stage of development: the powdery appearance is due to the spores. Nat. size.
- Fig. 4. One of the above buds completely destroyed by the fungus; the tissues are permeated in all directions by the close-set mycelium, and the whole is reduced to what practically resembles a sclerotium. Nat. size.
- Fig. 5. Portion of a thin section through a lily-bud in the condition of the lower ones of Fig. 1. The tissues of the bud are unrecognisable, as they are practically replaced by fungus-hyphae, forming a dense, tough felt-work of the nature of a stroma or sclerotium. Two tufts of conidiophores are seen, projecting from the surface. Zeiss B.
- Fig. 6. Portion of thin section across such a spot as that in Fig. 3, at the margin where the healthy and moribund tissues join. The dead and dying cells in and near the region attacked by the fungus, collapse and cause the whole to shrink. In the swollen cell-walls are the hyphae, cut across in all directions: these are already sending conidiophores to the exterior, and long hyphae down between the killed cells of the interior. Note the collapsed lumina and swollen walls of the latter. Zeiss B.
- Fig. 7. Portion of the last preparation more highly magnified, and showing more clearly the cut hyphae running in the substance of the cell-walls of the epidermis and other tissues. It also shows the base of young conidiophores, and the long, thin, almost vertical hyphae sent down between the cells of the interior. Zeiss D.
- Fig. 8. Portion of a transverse section through a sepal of the lily near a disease spot, but at a place just beyond the region actually occupied by the hyphae: the cell-walls are becoming swollen, discoloured, and disorganised, and the contents of the cells destroyed.
- Fig. 9. Group of conidiophores in various stages of development, growing into the damp air from the surface of the bud. A hypha (a) is protruded, and then (b) becomes septate, and puts forth a few branches; these branches swell at their ends (c), and develop minute peg-like protuberances at various points. Each of these pegs gives rise to a conidium, by swelling at its distal end into an oval body, which soon acquires the typical characters of a spore (c). Zeiss D.
- Fig. 10. Young hypha emerging through the epidermis of the petal of a lily. The development is very rapid, as will be seen later. Zeis D/a.
 - Fig. 11. Conidia, and their germination. To the left are two recently detached

conidia in water; the larger one measured $\frac{1}{10}$ mm. long by $\frac{1}{60}$ mm. broad. At a is a conidium germinating after lying three hours in water at the ordinary temperature; a' the same four and a-half hours later; a'' the same fifteen hours later still. Zeiss D.

Fig. 12. A similar culture in water. The conidium β was placed in water at 11.30 a.m. on July 7th; at 2.30 p.m. it had germinated as shown. β' the same at 7 p.m.; β'' the same at 10 a.m. next day (July 8); β''' the same at 7 p.m. on July 8th. It will be noticed that as the process of germination advanced, the protoplasm in the spore became very frothy, and finally passed entirely into the hyphae (e. g. β'' and β'''). Still later (β'''), the protoplasm in the hyphae also became vacuolated. On the 9th of July all growth had ceased, the culture remaining as shown in β''' , except that the vacuolation had increased: and by July 11th (i. e. after nearly five days in water) the septate hyphae contained little ut water and a few granules. The tip of the long hypha had swollen a little. All Zeiss D.

Fig. 13. A conidium germinating in water, in which a slice of a lily-bud had been placed; the influence of the food-material was at once evident from the outset in the more numerous and stronger branches, etc. The spore was sown on August 1st, at 4 p.m., and the drawing made August 2nd, 11 a.m. Zeiss D.

Fig. 14. Germination in Pasteur's solution. The spore α was sown on July 7, at 7 p.m., and when drawn (10 a.m., July 8th), had been germinating for 15 hours. Zeiss D.

PLATE XXI.

Fig. 15. The same conidium nine hours subsequently, the culture going on in a hanging drop of Pasteur's solution. Zeiss D.

Fig. 16. The same culture on July 9th at 8.30 a.m., i.e. 13½ hours subsequently. The drawing was made as exact as possible, but under a lower power (Zeiss B), in order to get the whole in. It will be noticed that at three places, marked x, cross-connections have been established between the hyphae.

Fig. 17. The same culture 48 hours later still, i. e. after four days from germination. A few of the ends of main hyphae have been omitted, but otherwise the courses of the branches are shown as correctly as possible: numerous cross-connections are observable, and certain small groups of tendril-like thin hyphae should be noted. The spore is still to be seen to the left below. Zeiss B.

Fig. 18. Two of the tufted groups of thin tendril-like hyphae of the above, more highly magnified. Zeiss D.

Fig. 19. A portion of the above mycelium, showing the cross-connections established by the fusion or conjugation of neighbouring hyphae. Note the remarkable case near x, where two short branches from below have curved over, and fused with one from above; while two other short branches, curving over still more towards the same point, have failed to establish the connection. Zeiss D.

Fig. 20. Portions of the mycelium of Fig. 11, showing the characteristic outlines of the tendril-like endings of the branches: the two slightly swollen ends, $\times \times$, are beginning to stick to the glass. Only the outlines are drawn, but the whole of the branches were full of bright protoplasm, and rapidly growing. Zeiss D.

Fig. 21. One of the curious swollen endings of hyphae in various stages of growth. The mycelium was three days old, and growing in Pasteur's solution. α was the condition at 2.30 p.m.; b=3.30 p.m.; c=6.30 p.m., and d=10.30 p.m.

It is these swollen, club-shaped endings which form the 'organs of attachment.' Zeiss D.

Fig. 22. One of the organs of attachment seen from above, as it adheres to the cover-slip from which the culture-drop was hanging. Its cell-walls deliquesce, and glue themselves flat on to the glass, as shown in profile in Fig. 23. Such an organ often puts forth a branch at × (Fig. 23), and goes on growing thence. Zeiss J.

Fig. 24. Three of the organs of attachment viewed from above, through the glass as before, showing how they may branch, and go on growing. Zeiss E.

Fig. 25. Young organs of attachment branching to form the tufts shown in Fig. 15 c. Zeiss D.

Fig. 26. Medium-sized (by no means the largest) tassel-like organs of attachment produced by the repeated branching of smaller ones. Zeiss D.

PLATE XXII.

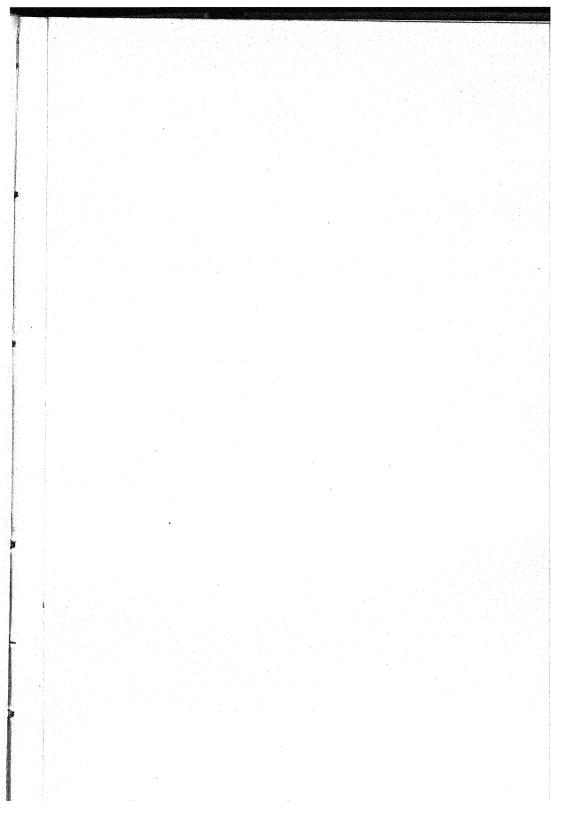
Fig. 27. The end of a hypha from the same mycelium as Fig. 15. α represents the condition of affairs at 7 p.m. on July 18; b=6.30 a.m. on the 19th; c=10 a.m. (19th); d=11.40 a.m.; e was drawn at 12.30; f at 12.45; g at 12.55; and h at 1.10 p.m. The chief point of interest is the gradual outgrowth of the branch. \times (in d), and its fusion with another one. The branch \times appeared as a slight protuberance about 11.30 a.m., and in 10 minutes presented the condition figured in d; at 12 o'clock the small branch opposite to it appeared, and was as shown in e at 12.30. It is noteworthy that the direction of the upper branch \times changed, and it curved so as to point the apex towards the new protuberance. As the two apices approached, the growth became more rapid, and at 12.55 (g) the tips were nearly in contact. Absolute contact took place at 1.3, as nearly as I could determine; at 1.10 the protoplasm of the two branches was continuous, as in h. The system was watched up to the evening, but no further changes of importance were noticed. Zeiss D.

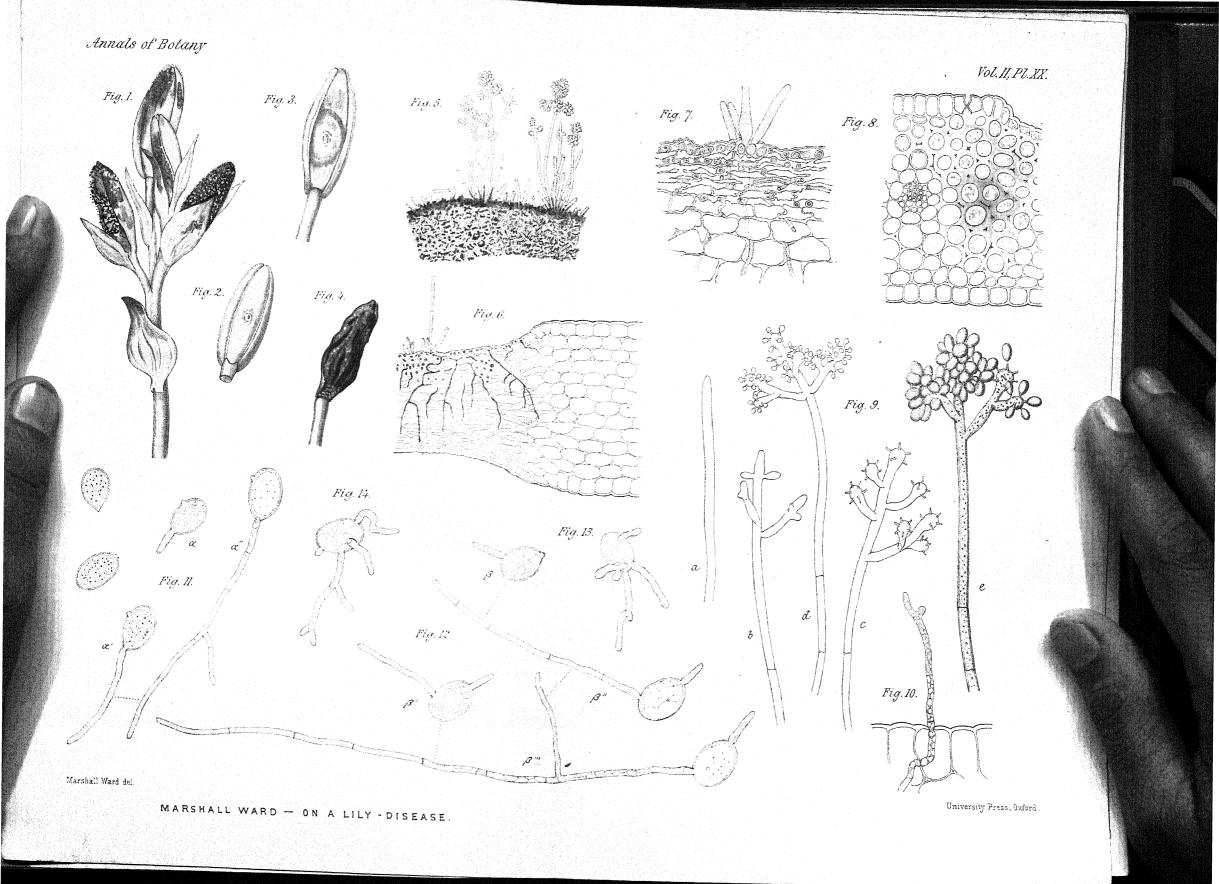
Fig. 28. Another case where the ends of two hyphae, at first growing at an angle, gradually turn so as to grow in the same straight line and fuse. a was drawn at 10 a.m., b at 10.45, and c at 12.30. As before, the protoplasm eventually became continuous by the fusion of the apices. Zeiss D.

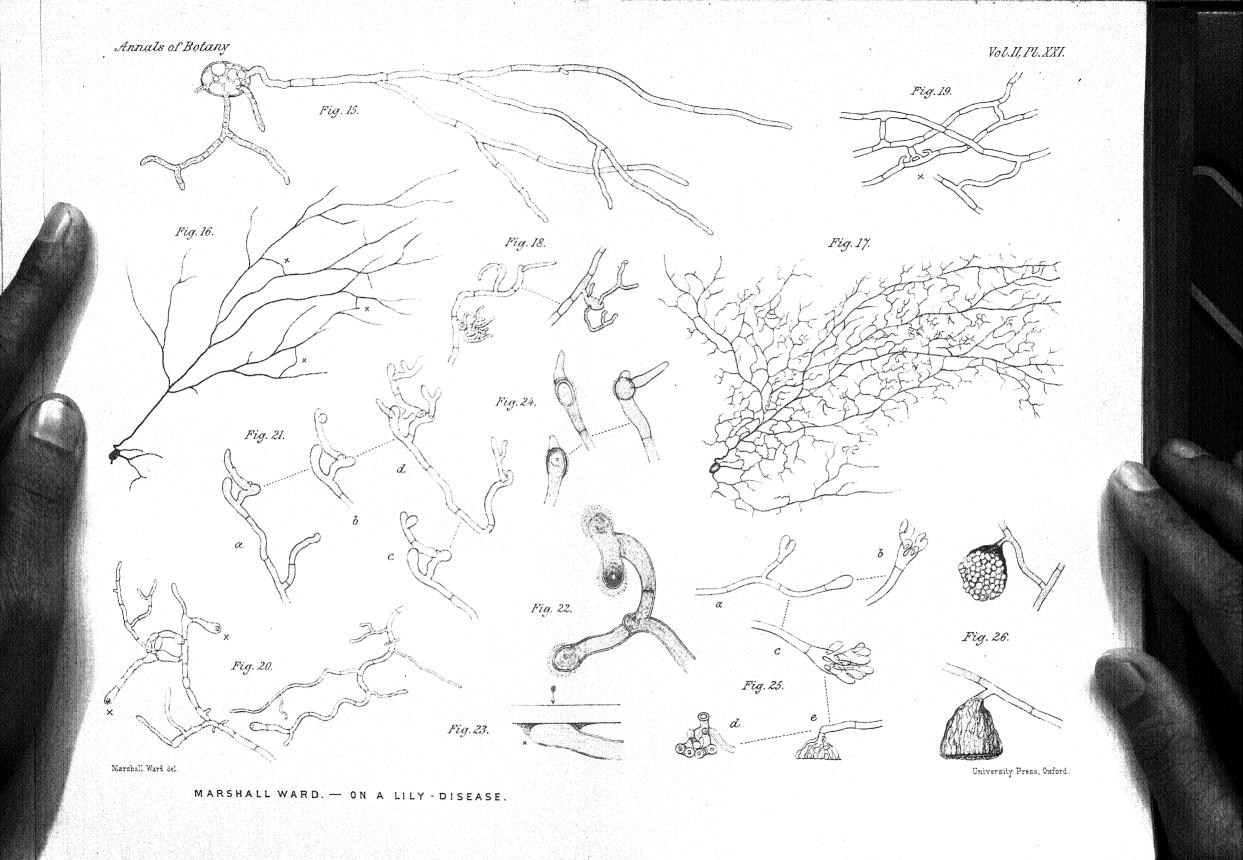
Fig. 29. Another case of the same kind, but less accurately timed. A was the condition of affairs at 4 p.m., and B was drawn at 8 p.m.; but it should be noted that the junction was already complete, at the point marked \times . Zeiss D.

Fig. 30. At 12.45 a junction was already established where the two hyphae cross at \times (in α), and just below two branches are growing out towards one another; to the right is a long, thin, straight hypha shooting across from another branch; at 2.25 the end of this straight hypha was in contact with one of the first-named branches (σ in β), and soon after it effected a junction. The effect of this was apparently to stop the further development of the two short branches near σ ; and they did not join. The mycelium from which this preparation was taken was cultivated in thick raisin-extract. Zeiss D.

Fig. 31. Taken from same mycelium as last. a was drawn at 4 p.m., and b at 4.10 p.m. The tip of the upper branch slid slowly along the lower branch, but no junction was established between them. In some cases junction is established eventually at the point of crossing after 24-48 hours. Such cases seem to prove that the hyphae must be in some special condition before they can establish junctions. Zeiss D.







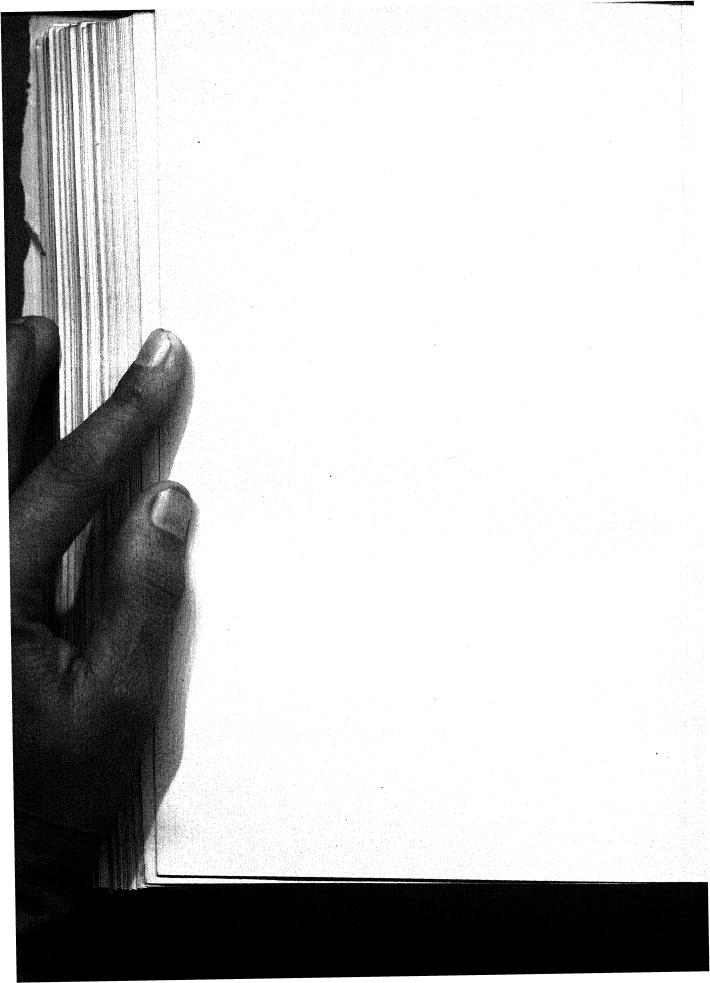


Fig. 32. A small culture of the fungus, from a single spore sown in a hanging drop: the medium was partially exhausted Pasteur's solution, and the culture was five days old. The original spore could still be seen in the meshes at s: the mycelium developed was not very large, but otherwise normal. Having nearly exhausted the food-materials, it passed over to the formation of conidiophores (c,c), seven of which are nearly completed. On the branches of the hyphae, especially at the edges and surface of the liquid where they are nearer to the air, numerous brilliant bubbles of gas are to be seen attached to the hyphae: this is a well-known phenomenon in such cultures, especially preceding the development of aërial conidia. It is, of course, not necessary to remark that these bubbles have nothing to do with the droplets extruded from the tips of hyphae described below. Zeiss A, oc. 2.

Fig. 33. Small conidiophores from a similar culture to the last, showing how the conidia may arise on short lateral branches, as well as on the normal erect conidiophores. The small branch (×) below the conidia grew out later into a secondary conidiophore similar to that in Fig. 26. Zeiss D, oc. 4.

Fig. 34. One of the conidiophores observed during its whole course of development. At 4.45 p.m. the erect hypha (*t*) was beginning to swell at the apex, and to put forth two branches below; these grew larger, and at 5 p.m. were as in 2. Half-an-hour later (i. e. at 5.30 p.m.) a number of small projections appeared like bright points on the swollen portions (*j*), and at 5.45 were seen to be peg-like outgrowths (*4*), which gradually lengthened, and commenced to swell at the ends (*s*, drawn at 6.5 p.m.) The swelling ends of these pegs (sterigmata) soon assumed the ovoid form of young conidia, and at 6.15 presented the appearance shown in 6. The development was now very rapid; 7 was drawn at 6.25, and by 6.40 the conidia were practically mature (*8*), the only further changes observable being the darkening in hue of the ripening conidia, which now drop off at the slightest vibration. The specimens were from a mycelium growing in Pasteur's solution, the solution having been again boiled; only the outlines are drawn, but it will be understood that all parts are filled with brilliant nearly homogeneous protoplasm. Zeiss D.

Fig. 35. Similar culture to the last, but showing the air-bubbles which are so common on the developing conidiophores, a, at 4.40 p.m.: b, at 5.25 p.m. Zeiss D.

Fig. 36. An aërial branch from a culture such as Fig. 21, showing the incrustation of minute crystals of calcium oxalate on the cell-walls. Zeiss D, oc. 2.

PLATE XXIII.

Fig. 37. A conidiophore from a 6 days' culture in Pasteur's solution, showing the formation of a second head of conidia from a branch below the one first developed. The culture was the same as that from which Fig. 15 was taken. The characteristic brownish colour of the quite mature spore and conidiophore has been omitted. Zeiss D, oc. 2.

Fig. 38. Branched conidiophore abundantly produced in the damp air of a culture-chamber: the mycelium had been growing for 14 days in a drop of raisin-extract, to which Pasteur's solution was added later. It should be noticed that the whole is a sympodium, each successive tuft arising at the end of a branch from beneath the one next below. Cf. Fig. 33 × and Fig. 37. Zeiss B, oc. 2.

Fig. 39. A young conidiophore from a culture in partially exhausted Pasteur's

solution. At 11.30 a.m. it presented the appearance shown in a, having six septa and a long growing segment above the sixth septum: at 3.20 p.m. this apical segment alone had grown to double its former length and had formed two new septa, as shown in b. Zeiss D, oc. 4.

Fig. 40. Further preparations giving some information as to the growth of the filaments. In α , the hypha lay just above a very thin section of epidermis, at 2.55 p.m. At 3.5 p.m. the tip of the hypha had moved forward as shown in b: at 3.30 p.m. the tip had progressed further still, having passed over the distance shown in c, and a small lateral branch had begun to form below. A comparison of the figures suggests that the apex described a slightly sinuous course, or very open spiral: it will be understood that the section of epidermis (part of a much larger piece) lay in a deeper plane. Zeiss D.

Fig. 41. The hypha a, crossing the one b, was in the position figured—relative to the diamond-shaped intercellular space towards which its tip is pointing—at 3.2 p.m., and it traversed the distances marked by $\times \times$ in ten minutes, reaching the first \times at 3.7, and the second \times at 3.12. Zeiss D.

Fig. 42. Three characteristic groups of terminal branches of a mycelium grown for a week in Pasteur's solution: the whole mycelium was produced from one spore At the points marked x, the ends of the hypha are seen to give off each a small cloudy drop. This, when first excreted, is a transparent, apparently mucilaginous drop, with very minute brilliant granules in it: as it ages, however, in a few hours it becomes more granular and has a yellowish hue. It gives proteid reactions, and the evidence goes to show that it contains a ferment which liquefies cellulose. Zeiss D.

Fig. 43. Similar excretions of drops from a culture in thin extract of raisins. Note the vacuolation of the hyphae. Zeiss D.

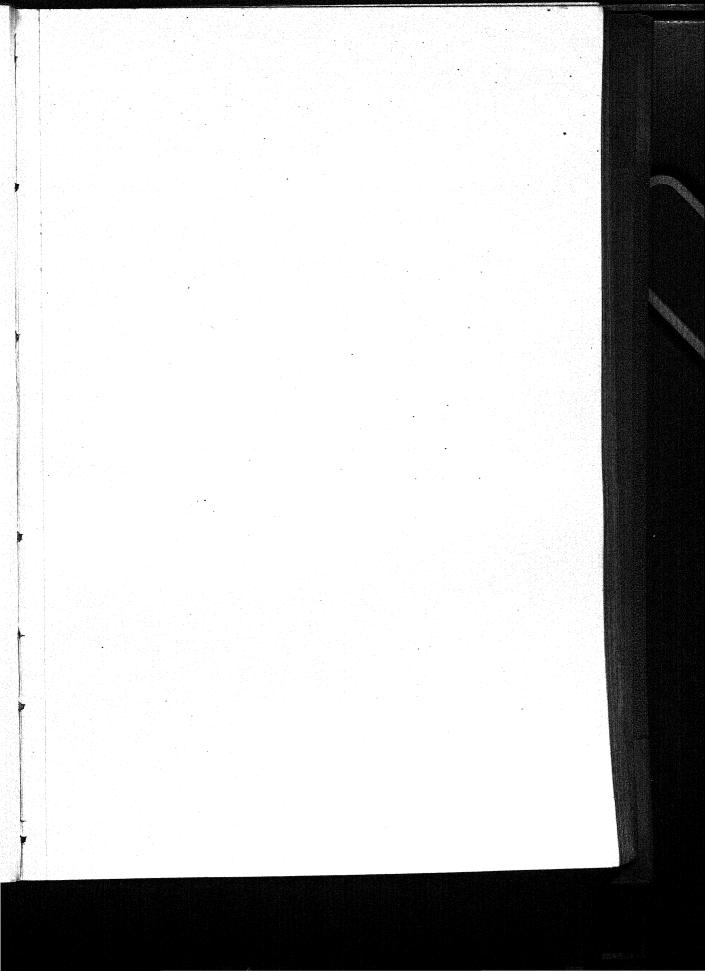
Fig. 44. Similar excretions of drops from hyphae of a large culture in Pasteur's solution (seven days after sowing). The preparation was taken from the edges of the large circular mycelium, which was a millimetre thick and nearly a decimetre in diameter: the excretion is much more copious in such pure cultures in flasks, with plenty of air and food-materials. Zeiss D, oc. 4.

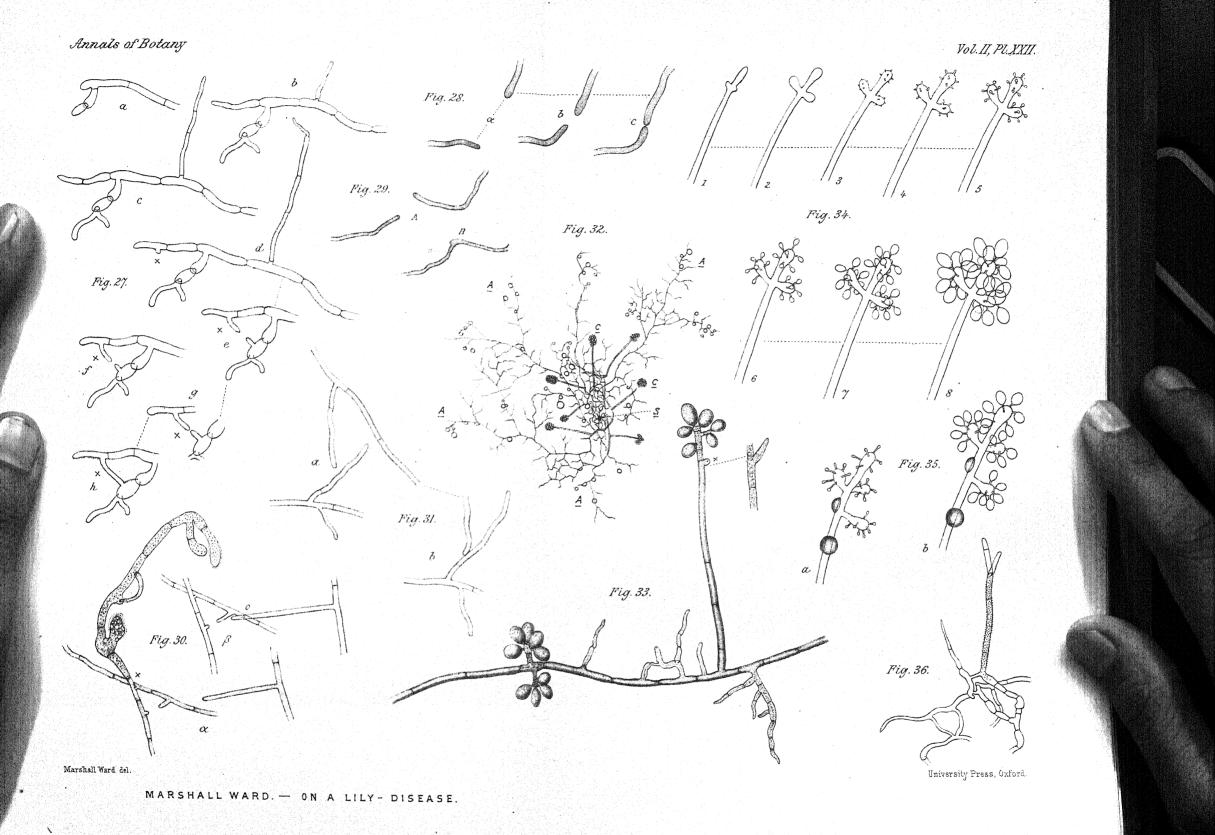
Fig. 45. One of the free hyphae of a strong culture shown in process of excretion of the drop. At first the protoplasm is bright and almost homogeneous (x); when the drop commences to exude, the protoplasm has been getting more and more vacuolated and granular (x); and this increases (x); until at length there may be very little protoplasmic content left (x); and the end may even collapse; but it frequently happens that the hypha goes on growing in the stage x, either putting out a bud-like outgrowth which becomes a branch, or itself going on growing. Zeiss J, oc. 3 and 4.

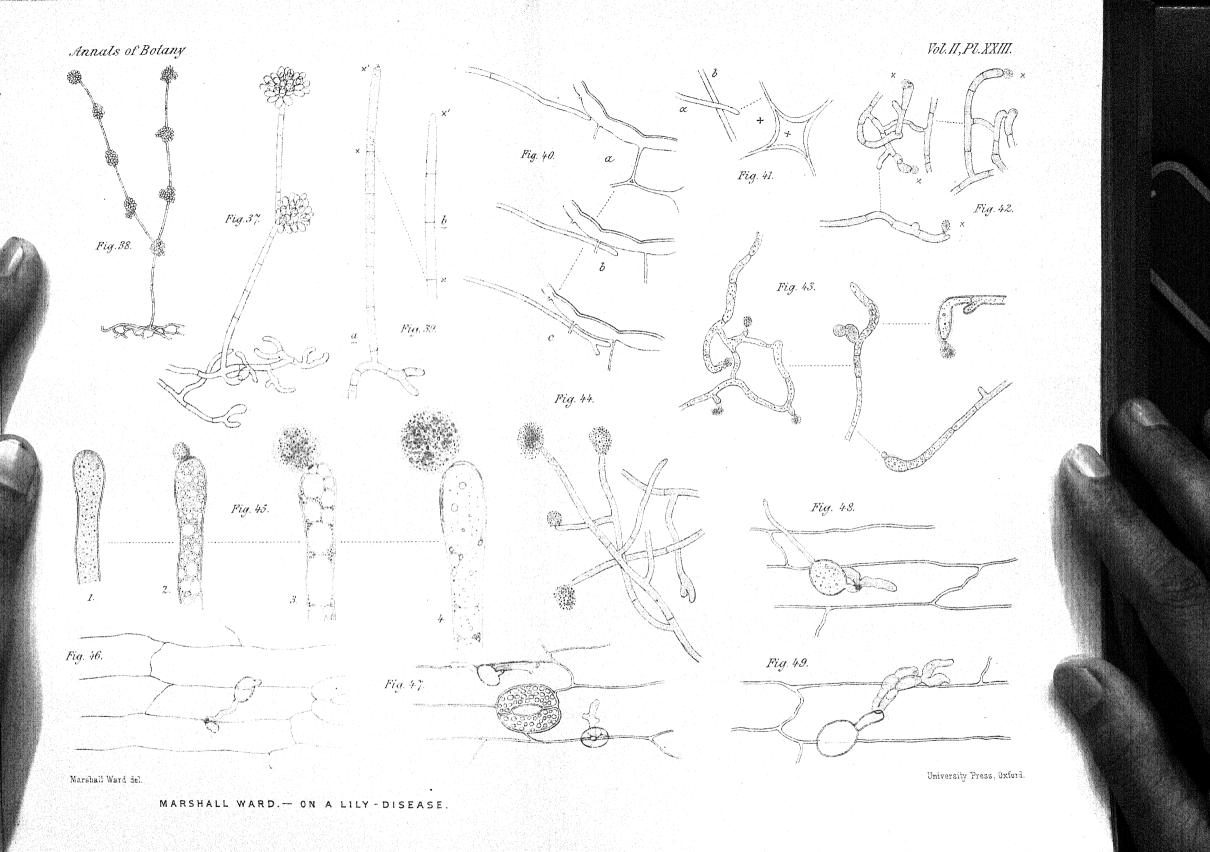
Fig. 46. Preparation showing the infection of the epidermis of a lily-bud. The conidium was placed on the bud in a drop of distilled water two days previously: it had germinated, and the tip of the longer tube attached itself closely to the cuticle and then discoloured and pierced it, the contents of the spore passing into the tube. The epidermal cells are only in outline. Zeiss D, oc. 2.

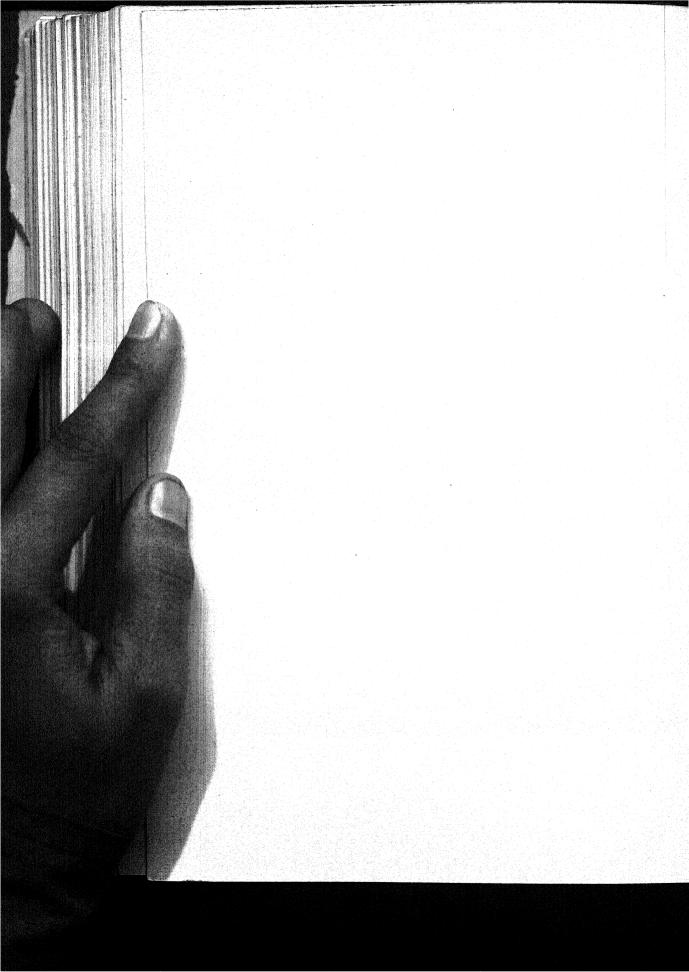
Fig. 47. Similar preparation, with two infecting conidia: in the upper one the whole of the protoplasm of the spore has already passed into the infecting tube, in the lower one some is still retained. Forty-eight hours' germination. As shown by











later preparations, these infecting tubes are running in the substance of the outer walls of the epidermal cells, just beneath the cuticle. Zeiss D, oc. 2.

Fig. 48. Similar preparation, but the conidium lay in a drop of dilute Pasteur's solution on the epidermis, and has thrown out a long thin hypha outside, in addition to the infecting tube below the cuticle. The spore still retained some protoplasm. Zeiss E, oc. 4.

Fig. 49. Similar preparation to the last, but the whole of the protoplasm has already passed into the infecting tube, which has become branched and septate. This preparation and the last were treated with chloral-hydrate before drawing. Zeiss E, oc. 4.

PLATE XXIV.

Fig. 50. Preparation showing a not uncommon mode of infection. The spore had germinated on the outside of the epidermis, and rapidly produced dense tufts of branching hyphae which make their way simultaneously into the tissues: the cell-walls around are all gelatinised, and turning brown. The preparation was made by cutting off the epidermis with the razor, and viewed from within. If seen in section (at right angles to the plane of the figure) the epidermis would be found sunk in, and turning brown, this could not be shown in the drawing. Zeiss D.

Fig. 51. Vertical section through a lily-bud with a 'disease spot' in the condition shown in Fig. 2. The epidermis and cuticle, together with underlying cells, have collapsed and turned brown: at first sight there are no signs of a fungus at this stage, but if such a section is carefully swollen by being treated with very dilute ammonia or chloral hydrate, the gelatinised cell-walls are found to have the fungus embedded in their substance. Zeiss D.

Fig. 52. A similar section to the above, but which has been swollen by holding it for a minute over an open bottle of ammonia hydrate. It is then seen that the walls of the epidermal cells and several subjacent cells are completely gelatinised and broken down, and that the fungus-hyphae are rampant in the mucilage. The destructive action is also seen to extend for some distance into the walls of neighbouring cells, as indicated by the yellow and red-brown hues which the destroyed walls assume. Zeiss D.

Fig. 53. Similar preparation to the last, but the section was taken through the pedicel, and the spot was in a slightly less advanced stage. The section was observed in water, in which the preparation (cut fresh) was laid: little can be made out beyond the fact that the cells are destroyed and the cuticle sunk; but it may be noticed that I had observed and drawn a sort of irregular dark mass, looking like a slight thickening of the cuticle about the middle of the depression—this was no doubt the collapsed remains of the spore.

In Fig. 54 the same section is shown after treatment with extremely dilute ammonia, and we now see that branched infecting hyphae were all the time embedded in the contracted mucilage produced by the destruction of the cell-walls: moreover, the empty spore which gave rise to these hyphae was still attached, and assumed its normal position after swelling in the ammonia. Again, and very clearly, it is seen that the destruction is extending into the walls of cells at a distance from the hyphae (cf. Fig. 8): it seems difficult to imagine how this can occur otherwise than by the diffusion of a soluble ferment, and investigation

shows that this explanation is no doubt the correct one. It will be noticed that the cuticle is not dissolved. Zeiss D.

Fig. 55. Part of a section through a lily-bud (perianth), on which the conidia had been allowed to germinate for three days, and which was thereby infected, as shown in Figs. 46-49. The section was cut from a bud which, after infection as said, was hardened in piero-nigrosin, and then absolute alcohol: it was then laid in glycerine, and held for a minute over the ammonia bottle. The left-hand guard-cell of the stoma and the whole of the section on the left were intact; but the five epidermis cells to the right of the stoma had collapsed under the pressure exerted by their gelatinised cell-walls, in the substance of which the hyphae are running. Further to the right, again, the cells are intact. The swelling action of the hyphae is beautifully seen in the walls below the right-hand guard-ceil. The swollen cell-walls in such sections still give a faint blue with chlor-zinc-iodine. Zeiss E, oc. 4.

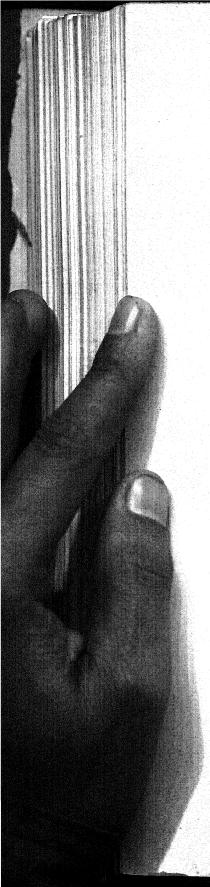
Fig. 56. Part of a similar preparation, perhaps slightly less advanced. All the essential features are as before. Zeiss E, oc. 4.

Fig. 57. Two stages showing the piercing of a cell-wall by the tip of a hypha. From a mycelium which had been growing for four days in a hanging drop, containing a minute section of a piece of lily-bulb. The hypha was observed to meet the cell-wall nearly at right angles: contact was established at 4.35, as seen in a. At 4.45, as seen in b, the tip of the hypha had dissolved a minute hole through the wall, passed through, and bulged out to its normal size on the opposite side. Zeiss D.

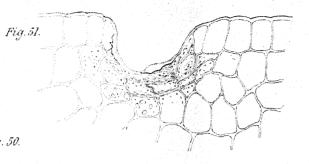
Fig. 58. Another case of the same kind, observed on Aug. 4. At 2.55 p.m. the hypha, which had traversed a drop of culture fluid (water containing a piece of lily-bulb), came vertically in contact with a cell-wall (a). The hypha was growing rapidly, and in three minutes its tip was seen to be deflected slightly (b=2.58)p.m.): this deflection increased—c was drawn at 3.0 p.m., and d at 3.2 p.m. At 3.7 p.m., the tip had obviously sunk into the substance of the cell-wall, which was swelling at the point of contact (c): the swelling of the wall and the sinking in of the tip of the hypha increased, and at 3.15 the tip of the hypha was nearly through, as shown at f. At 3.24 (g) a minute, bright, drop-like protuberance was being put forth on the other side of the cell-wall: this was a bud-like outgrowth continuing the onward growth of the hypha, as seen at h (3.28 p.m.) and i (3.30). All Zeiss D, oc. 4.

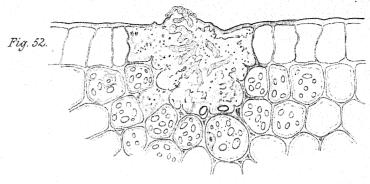
Fig. 59. Piece of thin transverse section of pedicel of lily after lying six hours in boiled extract from the fungus: the extract was made by pounding in a mortar a flask culture (in Pasteur's solution) of the fungus, with a little distilled water. Zeiss D.

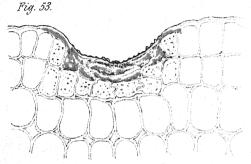
Fig. 60. A similar preparation, but which had lain for six hours in the unboiled extract from the fungus. Even after one hour, the cell-walls were observed to be swollen, and in six hours they were rapidly becoming disorganised: they still gave the blue reaction with chlor-zinc-iodine. Zeiss D.

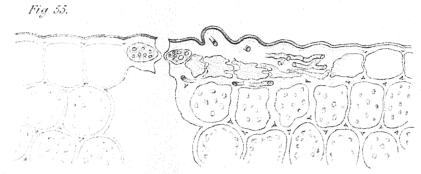


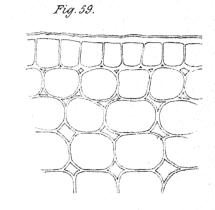


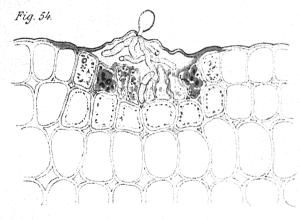


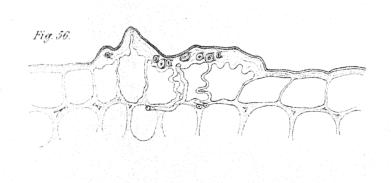


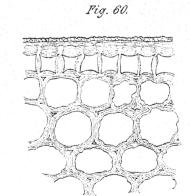


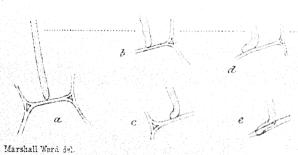


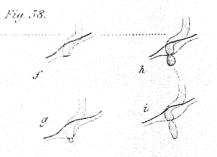


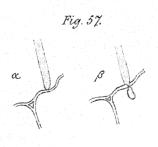












MARSHALL WARD. - ON A LILY-DISEASE.

NOTES.

APOSPORY IN PTERIS AQUILINA.—While at Squam Lake, New Hampshire, in July 1887, I noticed by the side of the road a plant of *Pteris aquilina* that presented a peculiar appearance which I, at first, thought must be due to the excessive heat then prevailing. Some of the pinnae were normal, but others were curled and irregular in shape with the margins somewhat thickened. I had no microscope with me at the time, and it was not until my return to Cambridge that I recognized that the sporangia on the abnormal

pinnae had developed in a peculiar manner, and that the present case was one of apospory, although not so well marked as similar cases described by Druery and Bower. As cases of apospory are not very common, an account of the peculiarities of the *Pteris* from Squam Lake may be of interest.

In the first place, an examination of the normal pinnae showed that the formation of sporangia had scarcely begun, and on none of them had the sporangia advanced so far as the formation of the archesporium. The appearance of the abnormal pinnae is shown in Fig. 17. A few of the sporangia on the abnormal pinnae were nearly mature and contained perfectly formed spores; but the greater part of the sporangia had, after the formation of the archesporium, developed abnormally. In some cases the normal development had ceased even before that stage was reached, and what should have been sporangia had developed

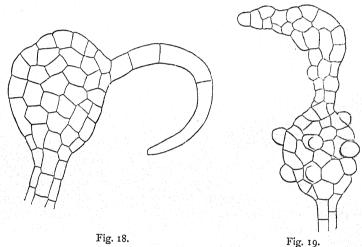


Fig, 17.

into sterile growths resembling, in some cases, moss-protonemata, in others, irregularly shaped prothalli. It should be remarked that the abnormal pinnae were most abundant at the tips of the different divisions of the frond, and the sporangia became more and more irregular the nearer they were to the tip.

In the majority of cases, immediately after the formation of the arche-

sporium, there grew from the apex of the sporangium a short filament; and sometimes two filaments grew out from the upper part of the sporangium diverging so as to form an angle of 45°. The terminal cell of the filaments was usually bluntly conical, the succeeding cells being cut off by walls at right angles to the axis of growth. In the simplest cases the filaments remained unbranched and composed of a single row of cells which usually became curved. In Fig. 18 is shown a case where the filament, whose cells contained abundant chlorophyll, might well be compared with a moss-protonema. In some cases the filaments had grown to double the length of that shown in Fig. 18.



More frequently, however, after the formation of the first two or three cells, the divisions were oblique and regularly placed, and, in some instances, the first partition itself was oblique and the subsequent divisions regularly oblique as in the tips of the narrow *Delesseriae*. As a rule, the filaments, even where oblique partitions were formed, remained nearly linear or cylindrical; but there were numerous cases where, by irregular division, a small prothalline body of a single layer of cells was formed. Such a growth is shown in Fig. 19, where it will be observed that a considerable number of the superficial cells of the aborted sporangium have grown outwards as if to produce other filaments or prothalli.

In a few cases, the initial sporangium had, at a very early stage, lost

all resemblance to true sporangia and, without reaching the stage at which the archesporium generally appears, had grown into a sort of irregular prothallus. Fig. 20 represents one of these prothalli, not at all to be confounded with the scales or paraphyses found in the sori of *Pteris*. In the particular case figured, a trace of what might possibly have been a small aborted archesporium could be seen a short distance below the terminal cell a. A secondary apical cell had

formed at δ , but it is impossible to surmise what its further growth would have been; it should, however, be remarked that, in some cases not here figured, there was not only a terminal prothalline growth, but also a lateral outgrowth of similar character from sporangia in which the normal development had advanced considerably farther than in the case shown in Fig. 20.

It is to be regretted that the subsequent growth of these prothalline structures could not be watched. At the time my speci-

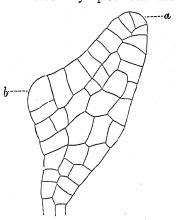


Fig. 20.

mens were gathered there was no trace of the formation of antheridia or archegonia; but it is not improbable that those organs might have developed later in the season. As it is, we have here another instance of the reversion of sporangia to structures which are, to say the least, prothalline in appearance. I have been informed by a person to whom my specimens were shown, that in a certain field in Pennsylvania the plants of Pteris frequently have an abnormal appearance like that shown in Fig. 17. It is to be hoped that hereafter some botanist, recognizing the peculiar deformity of Pteris here described, will be able to watch the development of the abnormal sporangial growths late in the season. It is certainly worthy of note that the abnormal pinnae bore some nearly mature sporangia at a season of the year when the normal pinnae showed only very young sporangia. One would ask whether the premature development and the accompanying abnormal growths were, in any way, the result of the extraordinary heat of the summer of 1887.

W. G. FARLOW, Cambridge, Mass.

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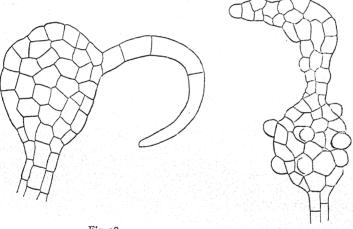


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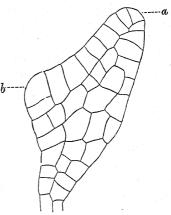


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ON THE RELATION BETWEEN THE FORMATION OF TUBERCLES ON THE ROOTS OF LEGUMINOSAE AND THE PRESENCE OF NITROGEN IN THE SOIL.—

At the meeting of the British Association in Manchester, 1887, I read a short paper on this subject describing certain water-culture experiments with the Bean (*Vicia Faba*), which tended to show that the development of tubercles is directly related to the absence of assimilable nitrogen in the surrounding medium. I now give a brief account of some further experiments with the same plant which confirm this conclusion. In both these experiments the Beans were grown in boxes containing well-washed sand.

Experiment I. This experiment was conducted in a greenhouse; one end of each box was exposed to direct sunlight, the other being always in the shade.

- 1888. Feb. 24. 130 seeds were selected; 65 of these were soaked in 1 litre of 1 p. cent. KNO₃ solution and 65 in water.
 - s, 26. The 65 seeds soaked in KNO₃ solution were sown in sand in one box (A), and the remainder of the solution was poured over the sand in the box. The 65 seeds soaked in water were sown in sand in another box (B).
 - " 28. Sprinkled 10 grams KNO₃ over sand in box A.

Mar. 5. First appearance of plants above ground.

7. Added to A: added to B:—

10 grams $MgSO_4$ 10 grams $MgSO_4$ 7. $Ca_3 = PO_4$ 10 grams $Ca_3 = PO_4$ 8. $Ca_3 = PO_4$ 10 grams $Ca_3 = PO_4$ 9. $Ca_3 = PO_4$ 10 grams $Ca_3 = PO_4$ 10 grams $Ca_3 = PO_4$ 11 grams $Ca_3 = PO_4$ 12 grams $Ca_3 = PO_4$ 12 grams $Ca_3 = PO_4$ 13 grams $Ca_3 = PO_4$ 14 grams $Ca_3 = PO_4$ 15 grams $Ca_3 = PO_4$ 16 grams $Ca_3 = PO_4$ 17 grams $Ca_3 = PO_4$ 18 grams $Ca_3 =$

, 23. Box A: added 10 grams KNO₃;

Box B: one plant pulled up and examined, no sign of tubercle on its roots.

Apr. 14. Examined from box A: 5 plants; no sign of tubercle, added 10 grams KNO...

,, B: 4 ,, tubercle on three.
,, 21. ,, A: 5 ,, no tubercle.
,, B: 5 ,, tubercle on all.
,, 30. ,, A: 6 ,, one plant with tubercle.
,, B: 6 ,, tubercle on all.

May 5. , A: 10 , one plant with tubercle.

May 5. Examined from box B: 10 plants; no case of tubercle.
(from shaded end of boxes.)
,, 12. ,, A: 10 plants; one with tubercle.
" B: 10 " three with tubercle
(shady).
,, B: 12 ,, eight with tubercle.
Summary. Of the thirty-six plants examined from box A, only
three had developed tubercles; whereas of the forty-eight plants
examined from box B, twenty-five had developed tubercles. There
was considerable mortality among the plants in box A; in box B,
several of the seeds failed to germinate.
Experiment II. The boxes in this case were in the open air in a
sunny situation, and were exposed to the rain.
1888. May 14. 50 bean-seeds were soaked for 48 hours in 700 cc. of
solution of 1 p. cent. KNO ₃ ; 50 seeds were soaked
in water for 48 hours.
,, 16. the 50 seeds soaked in KNO ₃ solution were sown in
sand in box A, and the remainder of the solution
was poured on the sand.
The 50 seeds soaked in water were sown in box B.
$_{\rm 3}$, $_{\rm 23}$. 13 grams KNO $_{\rm 3}$ added to A.
,, 30. IO ,, ,, ,, ,,
June 6. 10 ,, ,, ,,
,, 13. 10 ,, ,, ,,
" 22. Examined from box A: 12 plants, two had tubercle.
,, ,, B: 48 plants, all of which, ex-
cept one, a small weak
plant, had tubercle.
" 29. " " A: 12 plants, one had tubercle
on youngest roots.
July 6. ,, ,, A: 12 plants, two had tubercle
on youngest roots.
어마, 사람들 하는 어떻게 하는 것들은 사람들이 되는 사람들이 가는 어느 사람들이 되었다. 그렇게 하는 것이 나를 살아 가는 것이다.

Summary. Of the forty plants which developed in box A, only five produced tubercles; whereas 47 out of 48 in B produced tubercles.

Experiment III. After having removed the tuberculous plants from box B in experiment II, 50 seeds were sown in it on June 27, the same sand, to which 50 grams KNO₃ had been added, being used. July 17. examined one, free from tubercle.

, 18. added 20 grams KNO₃.

July 21. examined four, all free from tubercle.

" 25. added 10 grams KNO₃.

" 28. examined four plants, one with tubercle.

Aug. 1. added 10 grams KNO3.

- ,, 4. examined twelve plants, three with tubercle (on youngest roots).
 - 8. added 10 grams KNO₃.

" 11. examined fifteen plants, four with tubercle.

Summary. 36 plants were grown from the 50 seeds, and of these 8 produced tubercles.

Remarks. The results of all these experiments agree in showing that the development of tubercles is much less when nitrate is present in the soil than when it is absent. It is also indicated that as the amount of nitrate diminishes, the development of tubercles becomes more marked. In experiments I and II, the tubercles were first detected nine days after the last supply of nitrate; the soil having become in the meantime impoverished in nitrate by watering (Experiment I) or by rain (Experiment II). In Experiment III, although the supply of nitrate was continued to the last, the gradual development of tubercles may be accounted for by the exceptionally rainy season, in consequence of which the soil was impoverished very rapidly. In all cases in which tubercles made their appearance on the roots of plants which had been supplied with nitrate, they are exclusively developed on the youngest roots, especially on those near the surface of the sand; in that part of the soil, that is, which would naturally lose its nitrate most rapidly.

A remarkable fact is that noted in Experiment I, on May 5; the absence of tubercle in ten plants which had received no nitrate. As no parallel case occurred in Experiment II, in which the plants were fully exposed to the sun, it appears that the absence of tubercles in these plants is to be connected with their imperfect exposure to light. It may be that tubercle is only produced when the conditions of nutrition are highly favourable; that the development of tubercle is, in fact, intimately connected with the metabolic activity of the plant.

The special object of Experiment III was to investigate the possibly infective origin of tubercle. The sand in box B had contained during Experiment II forty-seven tuberculous plants; yet, in Experiment III, only eight plants out of thirty-six grown in the same sand were tuberculous. This experiment does not conclusively prove that

tubercular disease, if it be a disease, is not infectious; but it does clearly prove the influence of nitrate in the soil in diminishing the development of tubercles ¹.

S. H. VINES, Oxford.

ON THE DEVELOPMENT OF THE ENDOCARP IN SAMBUCUS NIGRA.—It is well known that those species of plants which produce succulent fruits are mainly indebted to animals for their means of dispersal, and it is necessary, in order that this end may be attained, that whilst the pulpy or fleshy portion of the fruit should be as attractive as possible, the seeds should be furnished with such characters as shall either prevent their being eaten at all, or shall enable them to pass through the alimentary canal with their powers of germination still unimpaired. This requirement is provided for, in by far the greater number of cases, by a hard envelope in which the seed or its essential parts are enclosed. These envelopes may be divided broadly into two classes, the one including those which are derived from a specially differentiated portion of the pericarp, and which is usually designated as the endocarp, the other comprising those coverings which, as in many true berries, form part of the seed itself.

It is to the former of these two classes that *Sambucus* belongs, the development of which it is the object of this note to describe.

If sections of the ovary of this plant be made while the bud is still very young, it is readily seen that the two innermost cell-layers which surround the 2-4 cavities containing the ovules are perfectly distinct both from each other and from those cells which lie immediately outside them, and that this difference is due to the peculiar mode in which cell-multiplication takes place in the two layers. In the innermost of these two layers, that which bounds the cavities of the ovary, the divisions occur regularly and exclusively in a plane at right angles to the long axis of the bud, that is, they are all transverse, whilst the few longitudinal divisions which mark the limits of the original cells do not increase in number at all. The impression which is gained of this layer taken as a whole, is that of a series of contiguous and hollow rings which bound the spaces destined eventually to contain the seeds. Each ring is of course divided internally into cells which correspond in number with the primary

¹ For a full discussion of this subject, and references to literature, see Ward, Some recent publications bearing on the question of the Sources of Nitrogen in Plants, in Annals of Botany, vol. i, 1887–8.

longitudinal divisions already mentioned (the figures will make the arrangement plain). The cells composing the outer of the two innermost layers behave, as regards their mode of cell-multiplication, in precisely the same way as those of the layer just described, with the difference that the plane of division is parallel with the long axis of the bud. The result of this is, that in a transverse section the cells of the inner layer which lie in the plane of the section







Fig. 22.

Endocarp of Sambucus nigra. Fig. 21, Transverse section from young bud. Fig. 22, Longitudinal section of a somewhat older stage. a, b, c, The layers forming the endocarp. d, Innermost layer of pulpy tissue.

appear as a segmented ring-like cylinder, whilst those of the outer layer resemble a circular chain, the links of which represent the cut ends of the cells whose greatest diameter is parallel with the long axis of the flower. In a longitudinal section this arrangement must evidently be entirely reversed (compare figures 21 and 22).

As development goes on, and as the bud increases in size, the primitive walls, which cut the cylindrical rings into segments, undergo a change of position becoming more and more oblique; and whilst the circular or elliptical form of the band as a whole remains unaltered, the individual cells composing it suffer a change of shape and are finally converted into elements with long pointed ends, the pointed portions slipping over each other in such a way that the thickness of the whole ring remains for a time fairly constant throughout. As a consequence of this, sections transverse to the

planes of the rings now show irregularities in the number of cut ends present at any part of it, and instead of being uniform in size and only one cell deep, the size is variable and the numbers may be from one to three,—a fact which shows how very considerable the overlapping of the ends must be, for as no tangential divisions ever

take place, the alterations are due entirely to the causes just described. At a later period in development the regular outline of the rings is distorted by the continued slipping of the ends, and the wavy outline of the older endocarp as a whole is partly to be attributed to this circumstance.

During the period of lengthening of the cells the nucleus, as might have been expected, undergoes a change in its appearance. From presenting an approxi-

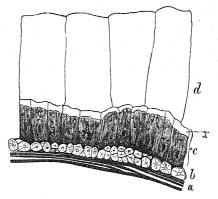


Fig. 23. Transverse section from nearly ripe fruit. a, b, c, The layers forming the endocarp. x, The unthickened portion of c in Figs. 21, 22. d, Innermost layer of pulpy tissue.

mately circular outline it becomes spindle-shaped and remarkably drawn out at the two ends; it is of a relatively large size, and the whole cell is very rich in protoplasmic contents—a feature which would of course be looked for in a tissue where metabolism is extremely active.

Meanwhile a third cell-layer, which lies immediately outside the two I have described, has undergone changes, preparatory to its taking part in the formation of the stone. And although the modifications which arise in it begin at a somewhat later period than those in the inner cells, they advance with great rapidity and soon cause this portion of the endocarp to be the most striking of all in appearance. The cells which compose it are much larger in transverse section (2–3 times) than those lying internally to it; but, like them, they are very densely filled with protoplasm in which a nucleus of a very large size is imbedded. The first change which takes place beyond mere increase in size, consists in a slight radial extension of the cells, and at the same time, just as in the case already described, the nucleus alters in form, becoming spindle-shaped, and lies at first somewhat

nearer the central end of the cells. Very soon after flowering, thickening of the cell-walls of each of the three layers commences. The mode of thickening, which the cell-walls of the two inner layers exhibit, does not differ from that common to ordinary sclerenchymatous tissues, and when completed the whole shows the usual stratification and pitted markings. The process is however a little more complicated in the outer layer, and recalls, in some degree, the manner in which the peristome of mosses is formed. Commencing at the central wall, the thickening deposit advances on the radial ones, but only extends to about four-fifths of the distance outwards towards the peripheral end of each cell, where it stops rather abruptly, and comparison of longitudinal and transverse sections shows that it is more strongly developed on the transverse than on the longitudinal walls. Bars and ridges of cellulose rise into the lumen of the cell both from the base, i.e. from the inner or central end of the cell, and also from numerous points on the radial walls. One result of the whole process is to drive the protoplasm, which suffers considerable diminution in bulk during the process, outwards towards the peripheral end of the cell, the thickening substance being itself meanwhile converted into an almost solid mass of extreme hardness. Transverse sections taken at a somewhat later period show the endocarp, which is very hard and lignified, to be apparently enclosed in a sheath of tangentially flattened cells (x, Fig. 23), an appearance which results from that peculiar absence of thickening in the peripheral regions of the cells of the third layer already referred to. It is not easy to arrive at a conclusion as to the use of such an unthickened portion. for it does not, as might be supposed, form a separation-limit, by which the stone is severed from the pulp when the fruit is ripe, but it becomes more and more indistinct as maturity is reached and is at length almost obliterated.

Although the stony endocarp has been treated of as enclosing the seed as a whole, it is in reality discontinued at that place where the placenta is found; and the passage immediately above this, which served for the entrance of the pollen tube, is also never completely filled up. It is probable that this weak spot is of importance in allowing the growing radicle to push its way out of the shell, which it would certainly experience considerably difficulty in doing, were the covering continued evenly round the seed as a whole.

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BOTANICAL NECROLOGY FOR 18881.

JOHANN ERIK EWALD ÄHRLING². Born at Bränkyrka in Södermanland, Sweden, September 18, 1837. Died at Arboga, April 5, 1888. Educated at Maria School and Gymnasium, Stockholm. Studied at the University of Upsala. Ph.D. 1872. Schoolmaster at Arboga, 1868–1888. Published:—

Studier i den Linnéanska nomençlaturen och synonymiken. Örebro, 1872.

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Caroli Linnaei opera hactenus inedita.

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HEINRICH ANTON DE BARY. Born at Frankfort-on-the-Maine, January 26, 1831. Died at Strassburg, January 19, 1888. Educated at the Gymnasium of Frankfort and the Universities of Heidelberg, Marburg, and Berlin. Graduated M.D. at Berlin, 1853. Docent at the University of Tübingen, 1853–55. Extraordinary Professor of Botany at the University of Freiburg i. Br. 1855–59. Ordinary Professor of Botany and Director of the

¹ In preparing the Necrology the Editors have been greatly assisted by Mr. George Murray, of the Botanical Department, British Museum.

² The editors are indebted to Prof. Blytt, of Christiania, and to Dr. Krok, of Stockholm, for information about Dr. Ährling.

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¹ The Editors are indebted to Prof. Magnus for information about Bauer.

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² The Editors are indebted to Prof. Caruel, of Florence, and Prof. de Toni for information about Bubani.

¹ The Editors are indebted to Prof. George Thoms, of Riga, and Prof. Magnus, of Berlin, for information about Prof. Bretfeld.

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¹ The Editors are indebted to Mr. Poisson, of Paris, for information about Hennecart.

² The editors are indebted to Dr. G. Krauss, of Stuttgart, for information about Lorenz Herter.

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¹ The editors are indebted to M. Duméril, of Toulouse, for information about Dr. Jeanbearnat.

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HUBERT LEITGEB². Born at Portendorf, Carinthia, October 23, 1835. Died at Graz, April 5, 1888. Educated at Gymnasium of Klagenfurt and University of Graz. Teacher of Natural History in the Gymnasium at Cilli, 1855–57; in the Gymnasium at Görz, 1857–64; in the Gymnasium at Linz, 1865; in the Gymnasium at Graz, 1866. Docent in the University of Graz, 1867; Extraordinary Professor of Botany in the University of

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JEAN BAPTISTE LIEURY ¹. Born at Rouen, December 14, 1888. Died at Rouen, September 3, 1888. Educated at College of Rouen. Biographical notice by Niel in Bulletin de la Société des Amis des Sciences Naturelles de Rouen, 1888. Published:—

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MENRI LORET². Born at Jarnac, Champagne, 1810. Died at Montpellier, December 4, 1888. Educated at Seminary of Pons. Biographical notice by Flahault in Bulletin de la Société Botanique de France, XXXV (1888). Published:—

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JOHN THOMAS IRVINE BOSWELL SYME (afterwards BOSWELL)¹. Born at Edinburgh, December 1st, 1822. Died at Balmuto, Fife, January 31st, 1888. Educated at Dollar Academy and University of Edinburgh. Civil Engineer. Curator of the Botanical Society of London, 1851. Lecturer on Botany, Charing Cross Medical School, 1854–1867, at the Westminster Medical School, 1855–1867, at the Free Church College, Edinburgh, 1868. Editor with Hewett Watson of 5th, 6th, and 7th editions London Catalogue of British Plants. Biographical notice by Baker, in Journal of Botany, 1888. Published:—

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² The Editors are indebted to the Secretary of the Société Botanique de Lyon for information about M. Therry.

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la Soc. des Lett. Sc. et Arts de l'Aveyroy le 23 juillet 1854.

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" — PHILIBERT: Étude sur le péristome (continued in Nos. 2, 3, and 4).

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- " BRIARD: Champignons nouveaux de l'Aube.
- " Flagey: Herborisations lichénologiques dans les environs de Constantine (Algérie).

" - PATOUILLARD: Sur quelques espèces de Meliola, etc.

Travaux des années, 1886-1887 Laboratoire d'Histologie du Collége de France.

VIGNAL: Recherches sur les micro-organismes de la bouche (Pl. I-VIII).

- ----: Recherches sur l'action des micro-organismes de la bouche sur quelques substances alimentaires.
- -----: Recherches sur les micro-organismes des matières fécales et sur leur action sur les substances alimentaires (Pl. XI et XII).

GERMANY.

Abhandlungen der senckenbergischen Gesellschaft zu Frankfurt a. M. Bd. XV.

GEYLER UND KINKELIN: Oberpliocänflora aus den Baugruben des Klärbeckens bei Niederrad und der Schleuse bei Höchst.

Noll: Experimentelle Untersuchungen über das Wachsthum der Zellmembran.

Annalen der Chemie (Liebig).

Bd. 243. HESSE: Beiträge zur Kenntniss der China-Alkaloide.

" 244. Schön: Ueber Nichtvorkommen der Hypogaeasäure im Erdnussöl.

Arbeiten aus dem kaiserlichen Gesundheitsamte zu Berlin. Ed. II (1887).

HOCHSTETTER: Ueber Mikro-organismen im künstlichen Selterwasser nebst einigen vergleichenden Untersuchungen über ihr Verhalten im Berliner Leitungswasser und im destillirten Wasser.

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SHIMOYAMA: Beiträge zur Kenntniss der Bukublätter.

Petersen: Beiträge zur Kenntniss der flüchtigen Bestandtheile der Wurzel und des Wurzelstocks von Asarum europaeum.

SCHMIDT UND HEUSCHKE: Alkaloïde der Wurzel von Scopolia japonica. HEUSCHKE: Ueber einige stickstofffreie Bestandtheile der Wurzel von Scopolia japonica.

SCHMIDT: Alkaloide der Scopolia Hlardnackiana.

WERNECKE: Das Caffein.

STROMEYER: Radix Ipecacuanhae pulverata.

Schäfer: Die Chinarinden aus den Plantagen im Gebiete des Mapiriflusses in Bolivien.

ITALLIE, VON: Ueber den Gerbsäuregehalt der Enzianwurzeln. Wilhelm und Schmidt: Über die Berberis Alkaloide.

SHIMOYAMA: Beiträge zur chemischen Kenntniss der Bukublätter.

BAUMERT: Bestandtheile des Lapinensamens.

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Heft 6. BAGINSKY: Demonstration zur reducirenden Wirkung der Bakterien.

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Bd. XLII.

ENGELMANN: Ueber Bakteriopurpurin und seine physiologische Bedeutung.

----: Ueber Blutfarbstoff als Mittel um den Gaswechsel von Pflanzen im Licht und Dunkeln zu unterscheiden.

SCHULZ: Ueber Hefegifte.

Bd. XLIII.

KRÜGER: Ueber den Schwefel der Eiweissstoffe.

Archiv für Hygiene (Forster, Hofmann, und von Pettenkofer).

Bd. VII (continued).

Heft 4. Birch-Hirschfeld: Ueber die Züchtung von Typhusbacillen in gefärbten Nährlösungen (Taf. V).

NAKAHAMA: Ueber den Rothwein- und Heidelbeerfarbstoff.

Bd. VIII.

Heft 1. BOKORNY: Ueber den Bakteriengehalt der öffentlichen Brunnen in Kaiserslautern.

Archiv für pathologische Anatomie und Physiologie (Virchow). Bd. CXI. LEWIN: Das Haya-Gift und das Erythrophlaein (Taf. XIII).

Berichte der deutschen botanischen Gesellschaft.

Jahrgang V (1887), continued.

Generalversammlung (II. Abth.).

Bericht über neue und wichtigere Beobachtungen aus dem Jahre 1886; abgestattet von der Commission für die Flora von Deutschland.

Jahrgang VI (1888).

Heft 1. TSCHIRCH: Ueber die Entwicklungsgeschichte einiger Sekretbehälter und die Genesis ihrer Sekrete (Taf. I).

"— REINKE: Die braunen Algen (Fucaceen und Phaeosporeen) der Kieler Bucht.

" — MÜLLER: Ueber phloëmständige Sekretkanäle der Umbelliferen und Araliaceen (Taf. II).

" - Wiesner: Zur Eiweissreaktion und Struktur der Zellmembran.

" — Schütt: Ueber das Phycoerythrin (Taf. III).

" — DIAKONOW: Ein neues Gefäss zum Cultiviren der niederen Organismen. (Mit einem Holzschnitt.)

" - Schumann: Einige Bemerkungen zur Morphologie der Canna-Blüthe.

" 2. OVERTON: Ueber den Conjugationsvorgang bei Spirogyra (Taf. IV)

" — LAGERHEIM: Zur Entwicklungsgeschichte des *Hydrurus*. (Mit 2 Holzschnitten.)

"— Ambronn: Pleochroismus gefärbter Zellmembranen (Vorläufige Mittheilung). (Mit 2 Holzschnitten.)

,, — MÜLLER: Zweimännige Zingiberaceenblumen. (Mit 2 Holzschnitten.)

" — MAGNUS: Ueber einige Arten der Gattung Schinzia, Naeg. (Mit einem Holzschnitt.)

" 3. KRAUSE: Ueber die Rubi corylifolii.

"— HILDEBRAND: Ueber die Bildung von Laubsprossen aus Blüthensprossen bei *Opuntia* (Taf. V).

Berichte der deutschen botanischen Gesellschaft (continued).

Heft 3. FISCHER: Zur Eiweissreaktion der Membran.

.. - ASCHERSON: Berichtigung.

" - BOKORNY: Ueber Stärkebildung aus verschiedenen Stoffen.

" — DIAKONOW: Eine neue Inficirungsmethode. (Mit einem Holzschnitt.)

"— LAGERHEIM: Ueber eine neue grasbewohnende *Puccinia*. (Mit einem Holzschnitt.)

. - ASKENASY: Ueber die Entwicklung von Pediastrum (Taf. VI).

" — Tschirch: Ueber die Inhaltsstoffe der Zellen des Aillus von Myristica fragrans, Hott (Vorl. Mittheilung).

" 4. REINSCH: Species et genera nova Algarum ex insula Georgia australi.

" — Höhml, von: Ueber das Material welches zur Bildung des arabischen Gummis in der Pflanze dient.

" - Klebahn: Ueber die Zygosporen einiger Conjugaten (Taf. VII).

" — VÖCHTING: Ueber den Einfluss der strahlenden Wärme auf die Blüthenentfaltung der Magnolia (Taf. VIII).

" 5. BUCHENAU: Doppelspreitige Laubblätter (Taf. IX).

" — Wiesner: Ueber den Nachweis der Eiweisskörper in den Pflanzenzellen.

, 6. WERMINSKI: Ueber die Natur der Aleuronkörner (Taf. X).

" — Palladin: Ueber die Eiweisszersetzung in den Pflanzen bei Abwesenheit von freiem Sauerstoff.

"— REINKE: Ueber die Gestalt der Chromatophoren bei einigen Phaeosporen (Taf. XI).

" - EBERMAYER: Warum enthalten die Waldbäume keine Nitrate?

" - HARTIG: Ueber die Wasserleitung im Splintholze der Bäume.

Berichte der deutschen chemischen Gesellschaft. Jahrgang XXI (1888).

No. 1. EINHORN: Beiträge zur Kenntniss des Cocains.

" 2. LIEBERMANN: Ueber das Nuclëin der Hefe und künstliche Darstellung eines Nuclëins aus Eiweiss und Metaphosphorsäure.

" 3. Ahrens: Zur Kenntniss des Sparteins.

" 4. Schön: Vorkommen der Oelsäure und nicht der Hypogäasäure im Erdnussöl.

, 5. Kreiling: Ueber das Vorkommen von Lignocerinsäure, $C_{24}H_4,O_2$, neben Arachinsäure, $C_{26}H_{46}O_2$, im Erdnussöl.

" 6. Petersen: Über das ätherische Öl von Asarum europaeum, L.

"— Bokorny: Über das angebliche Vorkommen von Wasserstoffsuperoxyd in Pflanzen- und Thiersäften.

" 7. Wurster: Aktiver Sauerstoff im lebenden Gewebe.

" - Tollens und Stone: Über die Gährung der Gelactose.

" 8. WILL: Über Atropin und Hyoscyamin.

" 9. Vogel: Über den Unterschied zwischen Heidelbeer- und Weinfarbstoff und über spektroskopische Weinprüfungen.

" - SCHMIDT: Umwandlung von Hyoseyamin in Atropin.

"— Bokorny: Zur Frage der Silberabscheidung durch lebende Zellen und deren angeblichen Zusammenhang mit dem Wasserstoffsuperoxyd.

"10. Thoms: Weitere Mittheilungen über die Bestandtheile der Kalumswurzel.

Berichte der deutschen geologischen Gesellschaft. Bd. XXXIX (1887). Felix: Untersuchungen über fossile Hölzer, III.

Bericht des naturhistorischen Vereins zu Augsburg.

HOLLER: Die Moosflora der Ostrachalpen.

BRITZELMAYR: Hymenomyceten aus Südbayern (Schluss).

Nachträge zur Flora von Schwaben und Neuburg, insbesondere neue Fundorte in der Umgegend von Augsburg.

Bericht der naturwissenschaftlichen Gesellschaft zu Chemnitz.

KRAMER: Über die Veränderung des Pflanzenbildes Europas durch die Einwirkung des Menschen.

ZIMMERMANN: Die Pisanggewächse.

KRAMER: Phytopaläontologische Beobachtungen.

Bericht über die Sitzungen der naturforschenden Gesellschaft zu Halle.

1887.

Kraus: Berichte über einige Arbeiten aus dem bot. Institute (Wille: Zur Diagnostik des Coniferenholzes; Menze: Zur täglichen Assimilation der Kohlehydrate: Eiselen: Ueber den systematischen Werth der Raphiden in dicotylen Familien).

Centralblatt, Biologisches.

Bd. VII (continued).

ZACHARIAS: Die feineren Vorgänge bei der Befruchtung des thierischen Eies.

HOFFMANN: Vererbung erworbener Eigenschaften. RICHTER: Zur Vererbung erworbener Eigenschaften. CARRIÈRE: Die Reblaus (*Phylloxera vastatrix*, Pl.).

Bd. VIII, Nos. 1-8.

LOEW UND BOKORNY: Die chemische Beschaffenheit des protoplasmatischen Eiweisses nach dem gegenwärtigen Stand ihrer Untersuchungen.

TARCHANOFF UND KOLESSNIKOFF: Ueber die Anwendung des alkalischen Albuminats des Hühnereies als durchsichtiges Substrat für Bakterienzüchtung.

SCHIESS: Uebertragung erworbener Eigenschaften.

 $\begin{array}{c} {\rm EngeLMANN:\ Ueber\ Bakteriopurpurin\ und\ seine\ physiologische\ Bedeutung.} \end{array}$

Pflanzen im Licht und Dunkeln zu unterscheiden.

WEISMANN: Botanische Beweise für eine Vererbung erworbener Eigenschaften.

HAACKE: Ueber zoologische Museen und die Regelung des naturkundlichen Museenwesens.

KORSCHETT: G. Haberlandt, Ueber die Beziehungen zwischen Funktion und Lage des Zellkerns bei den Pflanzen: nebst eigenen Mittheilungen.

Bos: Untersuchungen über Tylenchus devastatrix, Kühn.

Ludwig: Neue pflanzenbiologische Untersuchungen, 1. Verbreitungsmittel der Pflanzen, 2. Bestäubungseinrichtungen, etc.

BÜTSCHLI: Müssen wir ein Wachsthum des Plasmas durch Intussusception annehmen?

LUDWIG: Die Blütennektarien des Schneeglöckchens und der Schneebeere; Neue Beobachtungen Fritz Müller's über das absatzweise Blühen von Marica.

Centralblatt, Botanisches.

Bd. XXXIII. No. 1. Jankó, jun.: Equisetum albo-marginatum, Kitaebel. Juel.: Die Anatomie der Marcgraviaceen.

" 2. LINDMANN: Ueber die Bestäubungseinrichtung einiger skandinavischen Alpenpflanzen.

3. HANSGIRG: Einige Bemerkungen zum Aufsatze A. Tomaschek's, Ueber Bacillus muralis.

" Forsberg: Ueber die Geschlechtervertheilung bei Juniperus communis.

,, OLBERS: Ueber den Bau der Fruchtwand bei den Boragineen. WILLKOMM: V. F. Kosteletzky.

" 4. Murr: Ueber die Einschleppung und Verwilderung von Pflanzenarten im mittleren Nord-Tirol (continued in Nos. 5, 6, and 7).

" 5. LUNDSTRÖM: Ueber Mykodomatien in den Wurzeln der Papilonaceen (continued in No. 6).

" 6. Peter: Ueber die Pleomorphie einiger Süsswasseralgen aus der Umgebung Münchens.

" 7. HARZ: Ueber vergleichende Stickstoffdüngungsversuche.

" ----: Agaricus lecensis, n. sp.

"— Johanson: Studien über die Pilzgattung *Taphrina* (continued in Nos. 8 and 9).

"8. DÜNNENBERGER: Bakteriologisch-chemische Untersuchung über die beim Aufgehen des Brotteiges wirkenden Ursachen (continued in Nos. 9-13).

"— BECK: Geschichte des Wiener Herbariums (continued in Nos. 9, 10, and 12).

" 10. SOLEREDER: Ueber den systematischen und phylogenetischen Werth der Getässdurchbrechungen auf Grund früherer Untersuchungen und eigener neuer Beobachtungen.

"11. Tubeuf: Ueber die Wurzelbildung einiger Loranthaceen.

,, - ---: Eine neue Krankheit der Douglastanne.

"12. STRÖMFELT: Untersuchungen über die Haftorgane der Algen (continued in No. 13).

Bd. XXXIV.

No. 1. BECK: Geschichte des Wiener Herbariums (continued in Nos. 2-5).

" - Brotkerns: Musci novi transcaspici.

" 2. Godlewski: Einige Bemerkungen zur Auffassung der Reizerscheinungen an den wachsenden Pflanzen (continued in Nos. 3-7).

,, — WILHELM: Anton de Bary (continued in Nos. 3-8).

,, 7. HAUCK UND RICHTER: Phycotheca universalis (index to three first fascicles) (continued in Nos. 8, 9).

,, 8. Schilberszky, jun.: Aspidium cristatum, Sw. in Oberungam.

,, 9. TOMASCHEK: Ueber Bacillus muralis.

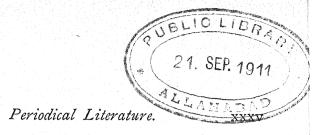
"10. RÖLL: Artentypen und Formenreihen bei den Torfmooren (continued in Nos. 11-13).

"11. Die Einweihung des botanischen Museums zu Breslau am 29 April, 1888 (continued in No. 12).

" — KRONFELD: Eine Vorrichtung zur Einschliessung mikroskopischbotanischer Präparate.

"13. MASSALONGO: Ueber eine neue Species von *Taphrina*. Centralblatt für Bakteriologie und Parasitenkunde Bd. III.

No. 1. BUJWID: Die Bakterien in Hagelkörnern.



Centralblatt fur Bakteriologie und Parasitenkunde (continued).

No. 1. HARTIG: Die pflanzlichen Wurzelparasiten (continued in Nos. 2, 3, and 4).

- " UNNA: Die Entwickelung der Baketerienfärbung (continued in Nos. 2-10).
- " 3. BUJWID: Bemerkungen über Sterilisation und Desinfection.
- "— Plaut: Zur Sterilisationstechnik. Mit I Abbildung (continued in No. 4).
- ,, 4. FISCHER: Ueber einen neuen lichtentwickelnden Bacillus (continued in No. 5).
- ,, 6. Kitt: Der *Micrococcus ascoformans* und das Mikofibrom des Pferdes (continued in Nos. 7, 8).
- ,, 7. EISENBERG: Bemerkungen über Kartoffeldauerkulturen nach der Methode des Prof. J. Sayka.
- ,, 8. Nonewitsch: Die Mikro-organismen einer enzootischen Leberentzündung by Ferkeln, Hepatitis enzootica porcellorum.
- ", 11. EISENBERG: Zur Aetiologie des Puerperalfiebers (continued in No. 12).
- " 12. SELANDER: Ueber die Bakterien der Schweinepest.
- "13. BAUMGARTEN: Bakteriologische Mittheilungen.
- ,, 14. Stenglein: Der mikrophotographische Apparat (continued in No. 15).
- " MENTSCHNIKOFF: Ueber die Bakteriologische Station in Odessa.
- "15. CHENZINSKY: Zur Lehre über den Mikro-organismus des Malariafiebers. STEINBERG: Streptokokken in einem Fall verruköser Endocarditis.
- "16. WEICHSELBAUM: Zusammenfassender Bericht über die Aetiologie der Tuberkulose (continued in Nos. 17–24).
- ,, 17. NEISSER UND JACOBI: Kleine Beiträge zur bakterioskopischen Methodik.
- "18. GRUBER: Notiz über die Widerstandsfähigkeit der Sporen von Bacillus subtilis gegen gesättigten Wasserdampf von 100° C.
- "— KITT: Ueber Abschwächung des Rauschbrandvirus durch strömende Wasserdämpfe (continued in No. 19).
- " 20. GRUBER: Erklärung der Desinfectionskraft des Wasserdampfes.
- "21. STENGLEIN: Versuche über mikroskopische Momentphotographie (continued in No. 22).
- ", 22. GIAXA: Ueber eine einfache Methode zur Reproduction der Koch'schen Kulturplatten.
- "23. FRAENKEL: Ueber die Kultur anaerober Mikro-organismen (continued in No. 24).
- Flora. Jahrgang LXXI, 1888.
 - No. 1. MULLER HAL.: Musci cleistocarpi novi.
 - " ARNOLD: Muellerella thallophila, Am. n. sp.
 - " 2. MÜLLER: Lichenologische Beiträge, XXVI (continued in No. 3).
 - " 3. SCHLIEPHACKE: Das Mikromillimeter.
 - " 4. KARSTEN: Ueber Pilzbeschreibung und Pilzsystematik (continued in No. 5).
 - " LAGERHEIM: Ueber eine durch die Einwirkung von Pilzhyphen entstandene Verietät von Stichococcus bacillaris, Näg.
 - " 6. ARNOLD: Lichenologische Fragmente, XXIX (continued in No. 7).
 - " 7. SCHULTZ: Vergleichende physiologische Anatomie der Nebenblattgebilde (Taf. I) (continued in No. 8).
 - " 9. MÜLLER: Lichenologische Beiträge, XXVIII.
 - ,, NYLANDER: Notiz über Parmelia perlata und einige verwandte

Flora (continued).

No. 10. CHODAT: Neue Beiträge zum Diagramm der Cruciferenblüthe (Taf. II).

" - REICHENBACH: Orchideae describuntur.

,, 11. HEINRICHER: Zur Biologie der Gattung Impatiens (Taf. III) (continued in No. 12).

"— Schliephacke: Ein neues Laubmoos aus der Schweiz (Bryum subglobosum, Schlieph).

" 12. DAMMER: Einige Beobachtungen über die Anpassung der Blüthen von Eremurus altaieus, Pall. an Fremdbestäubung.

" - Reinsch: Ueber einige neue Desmarestien.

,, 13. MÜLLER: Lichenologische Beiträge, XXIX.

" 14. HANSGIRG: Ueber die Gattungen Herposteiren, Näg. und Aphanochaete, Berth. non A. Br., nebst einer systematischen Uebersicht aller bisher bekannten oogamen und anoogamen Confervoideengattungen (continued in No. 15).

" 15 Schulz: Ueber Reservestoffe in immergrünen Blättern unter besonderer Berücksichtigung des Gerbstoffs (Taf. IV).

Forschungen auf dem Gebiete der Agriculturphysik (Wollny). Bd. X (continued).

Wollny: Untersuchungen über den Einfluss der Pflanzendecke und der Beschattung auf die physikalischen Eigenschaften des Bodens (Zweite Mittheilung). II. Der Einfluss der Pflanzendecke und der Beschattung auf die Bodenfeuchtigkeit. III. Der Einfluss der Pflanzendecke und der Beschattung auf die Siekerwassermengen im Boden.

: Untersuchungen über die Temperaturverhältnisse des Bodens bei verschiedener Neigung des Terrains gegen die Himmelsrichtung und gegen den Horizont (Nachträge).

SORAUER: Zur Charakteristik der Allicatio.

WOLLNY: Forstlich-meteorologische Untersuchungen. I. Untersuchungen über die Temperatur- und Feuchtigkeitsverhältnisse der Streudecke.

Forschungen zur deutschen Landes- und Volkskunde (Kirchhoff). Bd. III.

Borggreve: Die Verbreitung und wirthschaftliche Bedeutung der wichtigeren Waldbaumarten innerhalb Deutschlands.

Gartenflora. Jahrgang XXXVII.

Heft I. GRAEBENER: Planera Keaki, Sieb. (Abbild. 6-8.)

"— Alphabetisches Verzeichniss sämmtlicher im Monat Oktober 1887 beschriebenen neuen oder abgebildeten älteren Pflanzen mit kurzen Beschreibungen (for November in Heft 3, for December in Heft 5, for January 1888 in Heft 7, for February in Heft 9, for March in Heft 11).

" 2. REGEL: Cattleya velutina, Rchb. f., var. Lietzei, Regel (Taf. 1265).

" - Magnus: Natürliches Ankopuliren.

"— REGEL: Ballota acetabulosa, Benth.; Anemone pavonica, DC., \$\beta\$ fulgens, DC.; Phrynium variegatum, N.E. Brown (Abbild. 18-20).

" 3. REGEL: Sphaeralcea Emoryi, Torr. und Oxybaphus (Mirabilis) californica, Gray (Taf. 1266).

- REICHENBACH: Cypripedium callosum, Rchb. f. (Abbild. 22-23).

" - REGEL: Tulipa Leichlini, Rgl.

" ---: Nephrolepis rufescens, Prsl., var. tripinnatifida h. Veitch



Gartenflora (continued).

- Heft 4. REICHENBACH: Zygopetalum Wendlandi, Rchb. f. (Taf. 1267).
 - " HOFFMANN: Agave micracantha, Salm. (Abbild. 23-24).
 - " Aristolochia ridicula, N.E. Brown (Abbild. 30).
 - "— REGEL: Tulipa libanotica, Rgl.; Begonia Scharffiana, Rgl; Thyrsacanthus Lemairianus, Nees.
 - " 5. Philippi: Die Frühlingsvegetation von Colina in Chili.
 - " Regel: Pothuava nudicaulis (L.) Baker; Philodendron Andreanum, Dev. (Abbild. 33); Cryptanthus Morreniana, Regl., n. sp.
 - " 6. BORNMÜLLER: Populus Steiniana, Brnmllr. (Abbild. 37, 38.)
 - " REGEL: Nephthithys picturata, h. Bull. (Abbild. 40.)
 - " Über den Platanen-Husten.
 - " 7. REGEL: Gentiana calycosa, Griseb.: Statice eximia, Schrenk, var. turkestanica, Rgl. (Taf. 1270).
 - " WITTMACK: Quesnelia Enderi (Rgl.), Gravis et Wittm. (Abbild. 41-43).
 - " Elaeocarpus cyaneus, Sims. (Abbild. 44).
 - " 8. WITTMACK UND WEBER: Eichhornia crassipes (Mart.) Solms (Taf. 1271).
 - " GOETHE: Ueber das Drehen der Baumstämme.
 - " REGEL: Diastema picta, Rgl.
 - " 9. REICHENBACH, F., UND ORTGIES: Oncidium Jonesianum, Rchb. f. (Taf. 1272).
 - " GOETHE: Zur Bekämpfung des Apfel- und Birnenrostes.
 - ,, DAMMER: Stachys tuberifera, Vaud. eine neue Gemüsepflanze.
 - " 10. STEIN: Vitis pterophora, Baker (Taf. 1273).
 - " LINDBERG: Eine merkwürdige Euphorbia (E. aphylla, Brouss. Abbild. 59).
 - " SIEGERT: Exorcarpus cupressiformis, Labill. (Abbild. 60).
 - " II. REICHENBACH: Cattleya (Labrata) Gaskelliana, var. albescens, Rchb. f. (Taf. 1274).
 - " 12. REGEL: I. Bahia confertiflora, DC.; 2. Chaenactis tenuifolia, Nutt; Antirrhinum Nuttalianum, Benth. (Taf. 1275).
 - ,, Smilax glycophylla, Smith (Abbild. 74); Boronia serrulata, Smith (Abbild. 75).

Hedwigia. Bd. XXVII.

- Heft 1. KÜNDIG: Beiträge zur Entwicklungsgeschichte des Polypodiaceensporangiums.
 - " HARTIG: Trichosphaeria parasitica and Herpotrichia nigra.
 - ,, HAUCK: Neue und kritische Algen des adriatischen Meeres.
 - " -: Die Characeen des Küstenlandes.
 - " Frank: Über die Verbreitung der die Kirschbaumkrankheit verursachenden *Gnomonia erythrostoma*.
 - ,, 2. STEINHAUS: Analytische Agaricineenstudien.
 - " HARTIG: Zur Verbreitung des Lärchenkrebspilzes, Peziza Wilkommii.
 - " LAGERHEIM: Ueber die Anwendung von Milchsäure bei der Untersuchung von trockenen Algen.
 - " STEPHANI: Hepaticae Africanae (continued in Heft 3 and 4).

Heft 3 und 4.

- " Prantl: Anton de Bary, Nekrolog.
- "— HAUCK: Ueber einige von J. M. Hildebrandt im Rothen Meere und Indischen Ocean gesammelte Algen.

Hedwigia (continued).

Heft 3 and 4.

- " Wettstein, von: Zur Verbreitung des Lärchenkrabspilzes, Helotium Willkommii, Hart.
- ,, HARTIG: Zusatz zu dem vorstehenden Artikel.
- " Karsten: Symbolae ad Mycologiam Fennicam, Pars XXII.

Heft 5 und 6.

- " Klein: Berträge zur Technik mikroskopischer Dauerpräparate von Süsswasseralgen.
- "— HANSGIRG; Ueber die Süsswasseralgen-Gattungen Trochiscia, Ktz.

 (Acanthococcus, Lgrh.; Glochiococcus, De-Toni) und Tetraedron, Ktz. (Astericium, Corda; Polyedrium, Näg.; Cerasterias,
 Reinsch.)
- " KARSTEN: Bary's 'Zweifelhafte Ascomyceten' (figs. 1-3).
- " REHM: Ascomyceten, fasc. XIX.

Hefte, Botanische (Wigand's, Marburg).

Heft 3. WIGAND: Das Protoplasma als Fermentorganismus; Ein Beitrag zur Kenntniss der Bacterien, der Fäulniss, Gährung und Diastasewirkung, sowie der Molekularphysiologie.

Humboldt. 1888.

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- " 5. Ueber die Veränderungen, welche der Mensch in der Vegetation Europas hervorgebracht hat.

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" - ZACHMANN: Neue Standorte.

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BRISCHKE: Bericht über eine Excursion nach Hela während des Juli 1887.

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-- : Conservirungsflüssigkeiten für fleischige und saftige Pflanzentheile.

-----: Ueber sogenannte 'Jalappo' aus dem tropischen West-Afrika.

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: Ueber einige durch *Protomyces macrosporus*, Ung. erzeugte Pflanzenkrankheiten im nördlichen Kalkalpengebiete.

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 - ZIMPEL: Interessantere zum Theil bisher in der Umgegend von Hamburg noch nicht beobachtete Blüthenpflanzen.
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 - "— HASSACK: Über das Verhältniss von Pflanzen zu Bicarbonaten und über Kalkincrustation.
 - ,, DIETZ: Beiträge zur Kenntniss der Substratrichtung der Pflanzen.
 - ,, Klebs: Beiträge zur Physiologie der Pflanzenzelle (Taf. V-VI).
 - ,, CAMPBELL: The staining of living nuclei (in English).
 - ,, PFEFFER: Über chemotaktische Bewegungen von Bakterien, Flagellaten und Volvocineen.
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 - Heft 6. SCHULZE UND SELIWANOFF: Ueber das Vorkommen von Rohrzucker in unreifen Kartoffelknollen.
 - "— SCHULZE: Ueber den Nachweis von Rohrzucker in vegetabilischen Substanzen.
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 - No. 3. HENNINGS: Ueber das Conserviren und Präpariren von Hutpilzen.

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KITAESATO: Ueber das Verhalten der Typhus- und Cholerabaeillen zu säure- und alkalihaltigen Nahrböden.

SCHÜTZ: Der Streptococcus der Druse des Pferdes.

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Heft 1. HESSE: Bemerkungen zur quantitativen Bestimmung der Mikro-organismen in der Luft.

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BORDONI-UFFREDUZZI: Notiz über Leprabacillen.

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DE VRIES: Ueber eine neue Anwendung der plasmolytischen Methode.

FISCHER: Glycose als Reservestoff der Laubhölzer.

GREAT BRITAIN.

Album, Orchid.

Vol. VII. (continued) contains plates of-Cypripedium Morgianiae, Rchb. f.; Laelia cinnabarina, Lindley; Oncidium Lamelligerum, Rchb. f.; Houbletia odoratissma antiquiensis, Linden; Album, Orchid (continued).

Mesospinidium vulcanorum, Rchb. f.; Cattleya bicolor, Lindley; Dendrobium Macarthiae, Hooker; Laelia alba sulphurea, Rchb. f.; Phalaenopsis Esmeralda, Rchb. f.; Dendrobium luteolum chlorocentrum, Rchb. f.; Cattleya Bovoringiana, Veitch; Vanda suavis, Chatsworth var; Laelia anceps Scottiana; Thunia Veitchiana, Rchb. f.; Peristeria elata, Hooker; Aerides expansum Leoniae, Rchb. f.; Laelia anceps Stella, Rchb. f.; Mormodes pardinum, Bateman; Laelia elegans Morreniana, Rchb. f.; Dendrobium Kingianum album; Cattleya Harrisoniae violacea, Hort; Odontoglossum Vuylstekeanum, Rchb. f.; Schomburgkia undulata, Lindley: Dendrobium Fylchianum roseum, E. S. Berkeley.

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Vol. I (continued).

WOODWORTH: The apical cell of Fucus. (Pl. X.)

JOHNSON: The procarpium and fruit in *Gracilaria confervoides*, Grev. (Pl. XI.)

Green: On the germination of the tuber of the Jerusalem Artischoke (Helianthus tuberosus).

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CLARKE: On Acalypha indica, L. (Woodcut 6.)

THISELTON-DYER: Calcareous deposit in *Hieronyma alchorneoides*, Allem.

GARDINER: On the power of contractility exhibited by the protoplasm of certain plant cells.

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Vol. II.

No. V. LISTER: Notes on the Plasmodium of Badhamia utricularis and Brefeldia maxima. (Pl. I, II.)

MASSEE: A monograph of the genus Calostoma, Desv. (Mitremyces, Nees). (Pl. III.)

Acton: On the presence of sexual organs in Accidium. (Pl. IV A.)

Acton: On the formation of sugars in the septal glands of Narcissus.

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BATESON AND DARWIN: On a method of studying Geotropism.

VAIZEY: On Catharinea lateralis, Valzey (Catharinea anomala, Bryhn).
A New British Moss. (Pl. IV B.)

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OLIVER: On the structure, development, and affinities of *Trapella*, Oliv., a new genus of *Pedalineae*. (Pl. V–IX.)

VINES: On the systematic position of Isoëtes, L.

VAIZEY: Preliminary note on the development of Equisetum. MASTERS: Pinus monophylla.

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No. 13. xxix. Colonial fruit (continued).

, - xxx. Saccharine.

" 14. xxxi. Seeds of Herbaceous plants.

,, 15. xxxii. Forsteronia rubber (Forsteronia gracilis, Benth.).

" - xxxiii. Patchouli (Pogostemon Patchouli, var. suavis).

" - xxxiv. West African Indigo plants.

" - xxxv. Vanilla.

" - xxxvi. Streblus paper (Streblus asper, Lour.).

" - xxxvii. Urera fibre (Urera tenax, N. E. Br.) with plate.

,, - xxxviii. Tea (Camellia theifera, Griff.).

" 16. xxxix. New garden plants.

,, 17. xl. Ipecacuanha (Cephaelis Ipecacuanha, Rich.).

, — xli. Brazilian Gum Arabic.

., - xlii. Trinidad coffee.

" - xliii. Patchouli (Pogostemon Patchouli, var. suavis).

" - xliv. Cochin china vine (Vitis Martini, Planch.).

,, - xlv. Madagascar ebony.

,, - xlvi. Shantung cabbage (Brassica chinensis, L.).

,, 18. xlvii. Manufacture of Quinine in India.

, - xlviii. Job's Tears (Coix Lachryma, L. var. stenocarpa).

" - xlix. Ramie or Rheea (Boehmeria nivea, var. tenacissima).

, — l. Botanical station at Lagos.

,, 19. li. Rhabur grass (Ischaemum angustifolium, Hackel).

, — lii. Cayman Islands.

., — liii. Valonia in Cyprus.

, - liv. Prickley pear in South Africa.

, — lv. Star Anise (Illicium verum, Hook. f.).

Chronicle, Gardeners'. Series 3. Vol. III.

No. 54. REICHENBACH, F.: Aërides difforme, Wall; Eria bicolor, Lindl.

,, - Brown: Ficus Canoni, n. sp.; Catasetum pulchrum, N. E. Br.

" - BAKER: Albuca (Leptostyla) Allenae, n. sp.

,, - Brown: Veronica cupressoides and its allies. (Figs. 3-6.)

" 55. REICHENBACH, F.: Laelia Gouldiana, n. sp. or n. hybr.

" - W. B.: Bonatea speciosa.

" - MANDA: Cypripedium Picherianum, n. sp.

" — Picea ajanensis. (Fig. 10.)

" 56. REICHENBACH, F.: Dendrobium strebloceras, Rchb. f., Rossianum, n. var.;

Paphina cristata, Lindl., Modiglianiana, n. var.; Oncidium chrysoraphis, n. sp.; Aëranthus Grandidierianus, Rchb. f.

Chronicle, Gardeners' (continued).

No. 56. Rolfe: Marmodes pardinum, var. unicolor.

" - Coffee grown at Kew. (Fig. 12.)

" 57. REICHENBACH, F.: Oncidium chrysofs, n. sp.; Dendrobium Brymerianum, Rchb. f., histrionum, n. subsp.; Warrea bidentata, Lindl.

" - F. E.: Korolkowiadiscolor, Rgl.

- Fasciated Petunia. (Fig. 21.)
- ", 58. REICHENCACH, F.: Esmeralda bella, n. sp.; Maxillaria Hübschii, n. sp.; Catasetum tapiricipes, n. sp.; Schomburgkia rhionodora Kimballiana, n. var.
- , The Algerian Fir (Abies numidica). (Fig. 23.)

,, - Cycnoches chlorochilum. (Fig. 24.)

- , Anderson: Inarching the Vine and Mango. (Figs. 25, 26.)
- " 59. REICHENBACH, F.: Angraecum Sanderianum, n. sp.; Catasetum trulla (Lindl.) maculatissimum.
- " Rolfe: Cypripedium Galatea, n. hybr.; Coelogyne graminifolia, Pas. and Rehb. f.

,, - DIXON: Nepenthes. Notes.

- . The last of its race (Psiadia rotundifolia). (Fig. 31.)
- " 60. D.: Leontyce darwasica; Corydalis Ledebouriana.
- "— REICHENBACH, F.: Laclia anceps (Lindl.) radians, n. var.; Lycaste macropogon, n. sp.; Phalaenopsis Stuartiana bella, n. var.; Laclia superbens (Lindl.) decorata, n. var.; Odontoglossum + elegantius, n. lus. vel hybr. nat.
- " Oxera pulchella. (Fig. 34.) Biota Sieboldi. (Figs. 35, 36.)

" 61. BROWN: Origanum hybridum (Fig. 37).

" - Rolfe: Dendrobium chrysenne, n. sp.

- " REICHENBACH, F.: Masdevallia cupularis, Rehb. f.; Laelia anceps munda, Rehb. f. and L. anceps rosea, Rehb. f.
- " Weevils and their grubs (Fig. 39). Odontoglossum Piscatorii (Fig. 40).
- " 62. REICHENBACH, F.: Rodriguezia Bungerothii, n. sp.

,, - : Aëranthus trichoplectron, n. sp.

" - RIDLEY: Ponthieva grandiflora, n. sp.

,, - Fruitung of Brugmannsia lutea (Fig. 42).

- "63. REICHENBACH, F.: Phalaenopsis denticulata, n. sp.; Odontoglossum Boddaertianum, n. sp.
- " : Crassula lactea (Fig. 47); the Melon Pear (Solanum guatemalense, Fig. 49).
- " SMEE: New Zealand, its fruit and forest trees.

" - W.: Caryota sobolifera (Fig. 52).

- ,, 65. WATSON: Proliferation in Utricularia (Fig. 54).
- "— REICHENBACH, F.: Oncidium Kramerianum, Rehb. f., resplendens, n. var.; Odontoglossum dicranophorum, Rehb. f.; Cattleya labiata Percivalliana bella.
- " ROLFE; Laelia virens, Lindl.; Masdevallia culex.
- " : Holothrix Lindleyana (Figs. 55 and 56).

" 66. JENMAN: Eichhornias at Home.

Chronicle, Gardeners' (continued).

No. 66. BAKER: Agave (Euagave) Baxteri, n. sp.

- "— REICHENBACH, F.: Coelogyne humilis (Lindl.) albata, n. var.; Oncidium (Cirtochilum) detortum, n. sp.; Dendrobium macrophyllum (A. Rich.) stenopterum, n. var.
- " Jackson: Mexican fibre (Agave heteracantha).
- " 67. REICHENBACH, F.: Cynosorchis elegans, n. sp.; C. Lowiana, n. sp.
- " Jones: The crossing of Ferns (continued in No. 69).
- " J. O. W.: The Lacquey Moth (Fig. 63).
- ,, 68. The Forestry School at Cooper's Hill.
- ,, REICHENBACH, F.: Cypripedium Rothschildianum, n. sp.
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, — KJELLMANN: Skottets bygnat hos fam. Chordariaceae.

., - Lundström: Några iakttagelser öfver Calypso borealis.

" — NILSSON: Scirpus parvulus, Roem. et Sch. och dess närmaste förvandtskaper i vår flora.

,, - : Tvenne nye Rumex-hybrider.

" - RINGIUS: Några floristika anteckningar från Wermland.

,, - SKÅRMANN: Salix depressa + repens, Brunn.

., - TROLANDER: Växtlokaler i Nerike.

" 12. Andersson: Om Palmella uvaeformis, Kg. och hollsporerna hos Draparnaldia glomerata, Ag.

" — Dusin: Om några Sphagnumprof från djupet af sydsvenska tarfmossar.

,, — JOHNSON: Jaktlagelser rörande några torfmossar i södra Småland och Halland.

" — LAGERHEIM: Mykologiska Bidrag iv: Ueber eine neue Peronospora-Art aus Schwedisch Lappland.

" — Lundström: Om färglösa oljeplastider och oljedropparnes biologiska betydelse hos vissa Potamogeton-arter.

., — NEUMANN: Om tvenne Rubi från mellersta Halland.

, - STARBÄCK: Kritisk utreduing af Leptosphaeria modesta, Auct.

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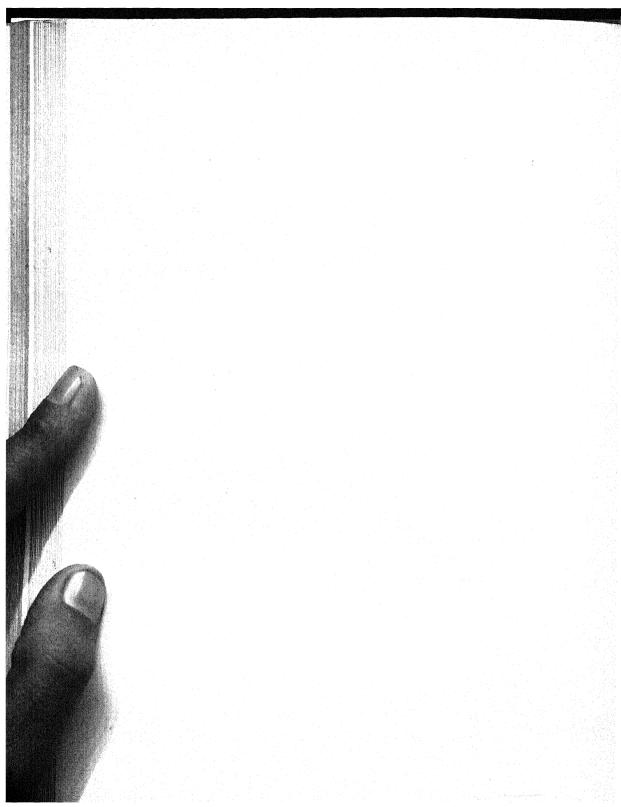
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- " BATTANDIER ET TRABUT: Excursion botanique dans le sud de la province d'Oran.
- " DEGAGNY: Origine nucléaire du protoplasma.
- ,, Cosson: De speciebus generis Polygala ad subgenus Chamachuxus pertinentibus.
- .. BORNET: Note sur une nouvelle espèce de Laminaire de la Méditerranée.
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" — KÜRNICKE: Bemerkungen über den Flachs des heutigen und alten Aegyptens.

" — STEINBRINCK: Ueber die Abhängigkeit der Richtung hygroskopischer Spannkräfte von der Zellwandstruktur (Taf. XIX).

" 9. DIETEL: Ueber eine neue auf Euphorbia dulcis, Jacq. vorkommende Melampsora.

, - BEAUVAIS: Ueber den anatomischen Bau von Grindelia robusta.

" 10. WIELER: Ueber den Ort der Wasserleitung im Holzkörper dicotyler und gymnospermer Holzgewächse.

" — Wortmann: Einige kurze Bemerkungen zu einer Abhandlung von Dr. Fr. Noll.

Generalversammlungs-Heft.

NECROLOGE :--

REES: Anton de Bary (mit Bildniss).

PFITZER: Robert Caspary.

FARLOW: Asa Grav.

HABERLANDT: Hubert Leitgeb.

MITTHEILUNGEN :--

Klebahn: Weitere Beobachtungen über die Blasenroste der Kiefern.

Büsgen: Ueber die Art und Bedeutung des Thierfanges bei Utricularia vulgaris, L.

ZACHARIAS: Ueber Entstehung und Wachsthum der Zellhaut.

Moeller: Anatomische Untersuchungen über das Vorkommen der Gerbsäure.

BEISSNER: Ueber Jugendformen von Pflanzen, speciell von Coniferen.

Frank: Ueber den Einfluss, welchen das Sterilisiren des Erdbodens auf die Pflanzen-Entwicklung ausübt.

Berichte der deutschen botanischen Gesellschaft (continued).

KLEIN: Ein neues Exkursionsmikroskop.

----: Beiträge zur Morphologie und Biologie der Gattung Volvox (vorläufige Mittheilung).

KIRCHNER: Ueber einen im Mohnöl lebenden Pilz (Taf. XIV).

Bericht über neue und wichtigere Beobachtungen aus dem Jahre 1887-Abgestattet von der Commission für die Flora von Deutschland.

Berichte der deutschen chemischen Gesellschaft. 1888. Nos. 11-18.

KOSSEL: Ueber eine neue Base aus dem Pflanzenreiche (aus Thee).

LIEBERMANN: Ueber ein Nebenalkaloid des Cocaïns, das Isopropylcocaïn.

ABBOT UND TRIMBLE: Ueber das Vorkommen fester Kohlenwasserstoffe in Pflanzen.

GUTZEIT: Ueber das Vorkommen fester Kohlenwasserstoffe im Pflanzenreiche.

EINHORN: Weitere Untersuchungen über das Cocaïn.

FRAGNER: Ein neues Alkaloid 'Imperialin' (aus Fritillaria imperialis).

JAHNS: Ueber die Alkaloïde der Arecanuss.

LIPPMANN: Ueber einige seltenere Bestandtheile der Rübenasche.

Bericht über die Senckenbergische Naturforschende Gessellschaft in Frankfurt a. Main. 1888.

JÄNNICKE: Die Gliederung der deutschen Flora.

Bibliotheca Botanica. Heft 12.

STENZEL: Die Gattung Tubicaulis, Cott. (Mit 7 Tafn.).

Centralblatt, Biologisches. Bd. VIII.

No. 9. HAACKE: Das Endergebniss aus Weismann's Schrift: 'Ueber die Zahl der Richtungskörper und über ihre Bedeutung für die Vererbung.'

,, 10. RICHTER: Zur Vererbung erworbener Charaktere.

" - Prazmowski: Ueber Sporenbildung bei den Bakterien.

" — ROSENTHAL UND SCHULZ: Ueber Alkali-Albuminat als Nährboden bei bakteriologischen Untersuchungen.

" 11. HAACKE: Weismann's Richtungskörpertheorie.

,, 12. EIMER: Die Entstehung der Arten auf Grund von Vererben erworbener Eigenschaften.

"15. RASKIN: Zur Züchtung der pathogenen Mikro-organismen auf aus Milch bereiteten festen und durchsichtigen Nährböden.

" 16. LUDWIG: Ueber weitere pflanzenbiologische Untersuchungen. Schutzmittel der Pflanzen.

" — Brock: Einige ältere Autoren über die Vererbung erworbener Eigenschaften.

,, - QUINCKE: Ueber Protoplasmabewegung.

,, 17. MIGULA: Die Verbreitungsweise der Algen.

,, - KRONFELD: Neuere Beiträge zur Biologie der Pflanzen.

" - ZACHARIAS: Landplanarien auf Pilzen.

,, 18. SCHULZ: Ueber Huminsubstanzen (continued in No. 19).

" - ROSENTHAL: Die Malaria und die Mittel zu ihrer Bekämpfung.

"19. LUDWIG: Weitere Untersuchungen über Ameisenpflanzen.

Centralblatt, Botanisches. Bd. XXXV.

No. 1. Petersen: Ueber Quernetze in Gefässen.

"— LUNDSTRÖM: Ueber die Salix-Flora der Jenesseij-Ufer (continued in Nos. 2-4).

,, 2. HANSGIRG: Ueber Bacillus muralis, Tomaschek, nebst Beiträgen zur Kenntniss der Gallertbildung einiger Spaltalgen (continued in Nos. 3, 4).

Nos. 3, 4.

EICHELBAUM: Mykologische Beobachtungen.

" — STARBÄCK: Einige kritische Bemerkungen über Leptosphaeria modesta.
Auctt.

Nos. 5, 6.

Keller: Wilde Rosen des Kantons Zürich (continued in Nos. 7-10).

" — LUNDSTRÖM: Ueber farblose Oelplastiden und die biologische Bedeutung der Oeltropfen gewisser *Potamogeton*-Arten.

" - BERGGREN: Ueber Apogamie des Prothalliums von Notochlaena.

" - LJUNGSTRÖM: Eine Primula-Excursion nach Möen.

No. 7. TOMASCHEK: Ueber eine angeblich neue Methode die Keime einiger niederen Algenpilze aus dem Wasser zu isoliren.

" 8. Areschoug: Ueber *Trapa natans*, var. *conocarpa*, F. Aresch. und ihre Abstammung von der typischen Form (continued in No. 9).

,, 10. Johanson : Einige Beobachtungen über Torfmoore im südlichen Schweden.

" II. WENZIG: Nova ex Pomaceis.

"— Istvánffi: Ueber das Präpariren der Pilze für wissenschaftliche Zwecke (continued in Nos. 12, 13).

"— Andersson: Ueber *Palmella uvaeformis*, Ktzg. und die Dauersporen von *Draparnaldia glomerata*, Ag.

" — Dusen: Ueber einige Sphagnum-Proben aus der Tiefe südschwedischer Torfmoore.

Bd. XXXVI.

No. 1. Bornmüller: Beiträge zur Kenntniss der Flora des bulgarischen Küstenlandes (continued in Nos. 2-5).

,, - Keller: Doppelspreitige Blätter von Valeriana sambucifolia, Mik.

,, 3. BROTHERUS: Musci novi exotici.

"— Kronfeld: Bemerkungen zu Herrn Dr. Istvánffy's Aufsatz: 'Ueber das Praepariren der Pilze', etc.

" 6. TOMASCHEK: Ueber Bacillus muralis und Zopf's Coccen und Stäbchenzoogloea der Alge Glaucothrix gracillima.

" 7. Prazmowski: Ueber die Wurzelknöllchen der Leguminosen (continued in Nos. 8, 9).

" 9. HARTIG: Untersuchungen über den Lichtstandszuwachs der Kiefer.

" - ---: Zur Verbreitung der Lärchenkrankheit.

" - Peter: Ueber die Pflanzenwelt Norwegens.

,, — ALLESCHER: Ueber einige aus Süd-Bayern bisher nicht bekannte Pilze (continued in Nos. 10, 11).

"10. TEPPER: Bemerkungen über die Kangaroo-Insel und einige Charakterpflanzen derselben (continued in Nos. 11, 12).

"— GREVILLIUS: Bau des Stammes bei einigen lokalen Formen von Polygonum aviculare, L. (continued in Nos. 11, 12).

Centralblatt, Botanisches (continued).

- No. 11. SADEBECK: Neuere Untersuchungen über einige Krankheitsformen von Alnus incana und A. glutinosa.
 - ., -: Die Antheren der Clusiaceen.
 - ,, 12. HARZ: Ueber Bergwerkspilze (continued in No. 13).
 - " SKÅRMANN: Monströse Form von Salix depressa x repens, Brunner.
 - " 13. DINGLER: Die Mechanik der pflanzlichen Flugorgane.
 - "— HARTIG: Der Einfluss der Samenproduction auf Zuwachsgrösse und Reservestoffvorrath der Bäume.
 - " Tubeuf, von: Pestalozzia Hartigii.
 - ,, DINGLER: Kleinere Mittheilungen.

Centralblatt für Bakteriologie und Parasitenkunde. Bd. IV.

- BENDER: Ueber den Erysipelcoccus (Fehleisen).
- BABES: Ueber einige Apparate zur Bakterienuntersuchung.
- BUCHNER: Eine neue Methode zur Kultur anaërober Mikroorganismen.
- PLAUT: Ueber eine Verbesserung meiner Wassersterilisations-Flaschen.
- GAMALEÏA: Zur Aetiologie der Hühnercholera.
- SCHMELCK: Steigerung des Bakteriengehalts während des Schneeschmelzens.
- WEICHSELBAUM: Nachtrag zum zusammenfassenden Bericht über die Aetiologie der Tuberculose.
- Bartoschewitsch: Die feuerfesten Wattepfropfen für die bakteriologischen Probingläser.
- Weibel: Untersuchungen über Vibrionen.
- PERRONCITO: Chytridium elegans, n. sp.
- BONOME: Pleuro-Pericarditis und Cerebro-Spinal-Meningitis Serofibrinosa durch einen dem *Diplococcus pneumonicus* sehr ähnlichen Mikroorganismus erzeugt.
- Ludwig: Der braune Schleimfluss, eine neue Krankheit unserer Apfelbäume.
- BUCHNER: Ueber die vermeintlichen Sporen der Typhusbacillen.
- SOROKIN: Ueber Algophaga pyriformis, n. gen. et sp.
- Ludwig: Weiteres über den Schleimfluss der Bäume.
- TASSINARI: Experimentaluntersuchungen über die Wirkung des Tabaksrauches auf die Mikroorganismen im Allgemeinen und im Besonderen auf die krankheiterzeugenden.
- TENHOLT: Neue Studien über die Pebrine-Krankheit der Seidenspinner.
- BUJWID: Neue Methode zum Diagnosticiren und Isoliren der Cholerabakterien.
- BELFANTI UND PESCAROLO: Ueber eine pathogene Bacterium-Art, entdeckt im Tetanusmaterial.
- JANOWSKI: Ueber den Bakteriengehalt des Schnees.
- SCHMELCK: Eine Gletscherbakterie.
- Bujwid: Traubenzucker als die Ursache der Eiterung neben Staphylococcus aureus.
- SOROKIN: Parasitologische Skizzen.
- SEHLEN, VON: Kleine Beiträge zur bakteriologischen Methodik.
- Schottelius: Beobachtung kernartiger Körper im Innern von Spaltpilzen.
- BENECKE: Ueber die Mycorhiza.

Centralblatt für Bakteriologie und Parasitenkunde (continued).

FERRARI: Ueber das Verhalten von pathogenen Mikroorganismen in den subcutan einzuspritzenden Flüssigkeiten.

FRANK: Ueber den Untergang der Milzbrandbacillen im Thierkörper.

PFUHL: Zur Sporenbildung der Typhusbacillen.

Petri: Einfacher Apparat zum Einspritzen von Flüssigkeiten für bakteriologische Zwecke.

Flora. Jahrgang LXXI, 1888.

No. 16. WENZIG: Die Gattung Spiraea, L. (continued in Nos. 17, 18).

" — Schulz: Ueber Reservestoffe in immergrünen Blättern unter besonderer Berücksichtigung des Gerbstoffs.

" 17. Hansgirg: Ueber die aërophytischen Arten der Gattungen Hormidium, Ktz., Schizogonium, Ktz., und Hormiscia (Fr.) Aresch.

Nos. 19-21.

HABERLANDT: Die Chlorophyllkörner der Selaginellen (Taf. V).

GNENTZSCH: Ueber radiale Verbindungen der Gefässe und des Holzparenchyms zwischen auf einander folgenden Jahrringen dikotyler Laubbäume (Taf. VI).

Nos. 22-26.

KNOBLAUCH: Anatomie des Holzes der Laurineen (Taf. VII).

No. 27. MÜLLER HAL: Die Mooswelt des Kilima-Ndscharo.

Nos. 28, 29.

Teitz: Ueber definitive Fixirung der Blattstränge durch die Torsionswirkung der Leitstränge (Taf. VIII).

SCHRODT: Beiträge zur Oeffnungs-Mechanik der Cycadeen-Antheren (Taf. IX).

Nos. 30-32.

LINDAU: Ueber die Anlage und Entwicklung einiger Flechten (Taf. X). MÜLLER: Lichenes Portoricenses.

STEPHANI: Porella Levieri, Jack. et Stephani, n. sp.

No. 33. HANSGIRG: Beitrag zur Kenntniss der Algengattungen Entocladia, Reinke (Entonema, Reinsch ex. p., Entoderma, Lagrh., Reinkia, Bzi.? Peripligmatium, Ktz.), und Pilinia, Ktz. (Acroblasta, Reinsch) mit einem Nachtrage zu meiner in dieser Zeitschrift (1888, No. 14) veröffentlichen Abhandlung (Taf. XII).

MÜLLER: Revisio Lichenum Eschweilerianorum (continued in Nos. 34-36).

Nos. 34-36.

Velenovský: Zur Deutung der Fruchtschuppe der Abietineen (Taf. XI). Müller: Lichenologische Beiträge, XXX.

Forschungen auf dem Gebiete der Agriculturphysik (Wollny). Bd. XI.

Wollny: Electrische Kulturversuche.

RAMANN: Untersuchungen über Waldböden. I. Abhandlung.

Kraus: Das Wurzelsystem der Runkelrüben und dessen Beziehungen zur Rübenkultur.

Forst- und Jagdzeitung, Allgemeine. Juli 1888.

Brecher: Ueber den Anbau von Acer (Negundo) californicum.

HOFFMANN: Ueber den phaenologischen Werth von Blattfall und Blattverfärbung.

Gartenflora. Jahrgang XXXVII.

- Heft 13. Regel: Aster alpinus, L. β speciosus, Rgl., und Trichopilia Lehmanni, Rgl. (Taf. 1276).
 - KÜHN: Welche Samen der Levkoye bringen gefüllt blühende Blumen?
 - "— Alphabetisches Verzeichniss sämmtlicher im Monat April 1888 beschriebenen neuen oder abgebildeten älteren Pflanzen mit kurzen Beschreibungen (for May in Heft 15, for June in Heft 17, for July in Heft 19, for August in Heft 21, for September in Heft 23).
 - ., Riss: Ein Nelkenfeind (Anthomyia radicum).
 - ,, 14. REGEL: Zygopetalum brachypetalum, Lindl. β stenopetalum, Rgl. (Taf. 1277).
 - " KITTEL: Dendrobium (Dendrocoryne) speciosum, Smith (Abb. 85).
 - " BORNMÜLLER: Noch Einiges über Populus Steiniana und P. hybrida (Abb. 88).
 - ., Iberis Garrexiana, All. (Ib. sempervirens, Lap.) (Abb. 90); Galvesia juncea, Benth. (Abb. 91).
 - ,, 15. ZABEL: Polygonum baldschuanicum, Rgl. (Taf. 1278).
 - ., HENNINGS: Eine giftige Kaktee, Anhalonium Lewinii, n. sp. (Abb. 92 und 93).
 - " Bredemeir: Freesia refracta, F. W. Klatt, var. alba (Abb. 94).
 - ,, WITTMACK: Was ist Nidularium striatum und Makoyanum?
 - " 16. REGEL: Oncidium Lietzei γ aureo maculatum, Rgl. (Taf. 1279).
 - ., -: Ixora alba, L.; Pleurothallis platystachys, Rgl.
 - ", 17. SPRENGER: Narcissus pachybulbus, D.R.; Crocus Imperati, Ten., var. purpureus, Hort. Damm; Cyrthanthus Mackennii, Hook f. (Taf. 1280).
 - , 18. REGEL: Cattleya labiata, Lindl., var. magnifica, Rgl.; Quesnelia Wittmackiana, Rgl. (Taf. 1281).
 - , ZABEL: Beiträge zur Kenntniss der Gattung Staphylea, L. (Abb. 113, 114) (continued in No. 19, Abb. 117, 118).
 - , 19. WITTMACK: Stephanandra incisa (Thbg.) Zabel.
 - ,, 20. Araucaria Cunninghamii (Abb. 127).
 - . Stephanotis floribunda in Frucht (Abb. 128, 129).
 - " 21. SPRENGER: Begonia geranioides.
 - ,, Alnus glutinosa, L., var. laciniata, Ehrh. (Abb. 131).
 - ,, NAGY, VON: Syringa japonica und eine Uebersicht der Syringa-Arten.
 - " 22. STEIN: Eulophia maculata, Rehb. f. (Taf. 1285).
 - " Dammer: Beiträge zur Kenntniss der Fichtenformen.
 - ,, 23. REGEL: Echinocactus texensis, Hopfer (Taf. 1286).
 - .. LINDEMUTH: Ueber eine botanisch interessante Birnensorte (Abb. 137).
 - " 24. REGEL: Ein neues Zyopetalum: Z. Sanderianum, Rgl. (Taf. 1287).

Hedwigia. Bd. XXVII.

Heft 7 und 8.

NORDSTEDT: Einige Characeenbestimmungen. 1. Ueber einige Characeen im Herbarium des k. botanischen Gartens zu Berlin.
2. Ueber einige Characeen aus Puerto-Rico.
3. Ueber einige Characeen aus Deutsch-Süd-west-Afrika.

Heft o und 10.

MÖBIUS: Ueber einige in Portorico gesammelte Süsswasser- und Luftalgen.

Hedwigia (continued).

STEPHANI: Calycularia crispa, Mitten.

Hansgirg: De Spirogyra insigni (Hass), Ktz., nov. var. fallaci, Zygne-mate chalybeospermo, n. sp. et Z. rhynchonemate, n. sp. adjecto conspectu subgenerum, sectionum, subsectionumque generis Spirogyrae, Link. et Zygnematis (Ag.) de By.

KARSTEN: Fragmenta mycologica, XXIII et XXIV.

LAGERHEIM: Eine neue Entorrhiza.

Heft II und 12.

WARNSTORF: Revision der Sphagna in der Bryotheca europaea von Rabenhorst und in einigen älteren Sammlungen.

Stephani: Westindische Hepaticae. I. Hepaticae portoricenses. II. Hepaticae ex insulis St. Domingo et Domininica quas collegit Eggers.

DIETEL: Ueber einige auf Compositen vorkommende Rostpilze.

KLEBAHN: Beobachtung über die Sporenentleerung des Ahornrunzelschorfs, Rhytisma acerinum, Fr.

NAWASCHIN: Ueber das auf Sphagnum squarrosum, Pers. parasitirende Helotium.

Hefte, Botanische (Wigand's, Marburg).

Heft III, herausgegeben von E. Dennert.

WIGAND: Das Protoplasma als Fermentorganismus.

Humboldt. 1888 (continued).

PFEFFER: Ueber Anlockung von Bacterien und einiger andern Organismen durch chemische Reize.

HABERLANDT: Das Princip der Oberflächenvergrösserung im anatomischen Bau der Pflanzen.

REICHE: Ueber die Veränderungen, welche der Mensch in der Vegetation Europa's hervorgebracht hat, II.

LUDWIG: Ueber einige merkwiirdige Rostpilze.

Moewes: Ist die Schuppenwurz (Lathraea squamaria) eine thierfangende Pflanze?

BECK: Die neuesten Anschauungen über die Pflanzen der Steinkohlenzeit.

Moewes: Zur Biologie der Gattung Impatiens.

Keller: Atavistische Erscheinungen im Pflanzenreich.

Jahresbericht der naturhistorischen Gesellschaft zu Hannover.

Nos. 34-37.

ANDRÉE: Vaccinium macrocarpum, Ait.

: Pflanzenansiedlungen auf Neubruch.

HESS: Tabelle zur Bestimmung der dem Rettig und Radieschen schädlichen Insecten.

MEJER: Veränderung der Flora der Eilenriede in den letzten 30 Jahren. Jahresbericht des naturwissenschaftlichen Vereins der Rheinpfalz.

Landau, XLIII-XLIV.
BOKORNY: Kurze Mittheilungen über die Bakterien im Brunnenwasser.

----: Das Wasserstoffsuperoxyd und die Silberabscheidung durch aktives Albumen.

-----: Die Keimung der Samen.

-----: Ein chemischer Unterschied zwischen lebendem und todtem Protoplasma.

Jahresbericht der Schlesischen Gesellschaft für vaterländische Kultur. LXV, 1887. KASSNER: Ueber Lacturin. ---: Ueber das fette Oel der Hirsefrucht. POLECK: Ueber die flüchtigen Bestandtheile der Wurzel und des Wurzelstocks von Asarum europaeum. -: Ueber die chemische Natur des aetherischen Oels von Asarum canadense. COHN: Ueber die physikalischen Eigenschaften des Tabaschir. ---: Ueber Mandragora. --: Bericht über die Enthüllungsfeier der Göppertschen Büste auf der Breslauer Promenade. ENGLER: Ueber die Flora der Insel Socotra. FICK: Resultate der Durchforschung der schlesischen Phanerogamenflora (1887).HIERONYMUS: Ueber Tephrosia heterantha, Griseb. -: Ueber einige Algen des Riesengebirges. Krassnow, von: Versuch einer Entwicklungsgeschichte der Pflanzenwelt in Central-Thian-Schan. LIMPRICHT: Ueber Th. Gümpel's Beiträge zur Entwicklungsgeschichte der Laubmoose. PAX: Ueber die Blüthenbildung der Capparidaceae. Schröter: Beiträge zur Kenntniss der nordischen Pilze. SONNTAG: Ueber die Diatomeen der Umgegend von Wüste-Waltersdorf. STENZEL: Ueber Oderhölzer. STEIN: Ueber Flechten vom Congo und aus dem Orient und über Strophanthus Ledienii. Jahrbücher, Botanische (Engler). Bd. X. Heft 3. PAX: Monographische Uebersicht über die Arten der Gattung Primula (Schluss). " - ENGLER: Plantae Marlothianae; ein Beitrag zur Kenntniss der Flora Süd-Afrika's, II Dicotyledonae sympetalae (Taf. VII-X). " — DE CANDOLLE: Plantae Lehmannianae in Guatemala, Costa Rica, Columbia, Ecuador, etc. collectae: Piperaceae. " - SCHWACKE: Eine neue Olacinee (Tetrastylidium Engleri, Schwacke, n. sp.). 4. PALLA: Zur Kenntniss der Gattung Scirpus (Taf. XI).

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ter der Rubiaceen Südamerikas.

" - WARMING: Ueber Grönlands Vegetation.

(Taf. XII-XIV).

Heft 3. WENT: Die Vermehrung der normalen Vacuolen durch Theilung (Taf. VII-IX).

" - SCHUMANN: Ueber einige verkannte oder wenig gekannte Geschlech-

" - SOLEREDER: Beiträge zur vergleichenden Anatomie der Aristolochiaceen

nebst Bemerkungen über den systematischen Werth der Secretzellen und über die Structur der Blattspreite bei den Gyrocarpeen

" - SCHUMANN: Einige neue Ameisenpflanzen (Taf. X-XI).

" 4. WAKKER: Studien über die Inhaltskörper der Pflanzenzelle (Taf. XII-XV).

" — MÜLLER, CARL: Ueber den Bau der Commissuren der Equisetenscheiden (Taf. XVI-XX).

- Heft I. Koch: Zur Entwicklungsgeschichte der Rhinanthaceen (Rhinanthus minor, Ehrh.) (Taf. I).
 - " Loebel: Anatomie der Laubblätter, vorzüglich der Blattgrün führenden Gewebe (Taf. II und III).
 - " MÜLLER (Münden): Spectralanalyse der Blüthenfarben (Taf. IV-VI).
- Jahrbücher, Landwirthschaftliche (Thiel). Bd. XVII.
- Heft 4, 5. Schulze: Ueber die Bildungsweise des Asparagins und über die Beziehungen der stickstofffreien Stoffe zum Eiweissumsatz im Pflanzenorganismus.
 - " Kreusler: Zum Nachweis von Nitraten im Erdboden, etc.
 - " FRANK: Bemerkungen zu vorstehendem Artikel.
 - " PLATH: Ueber die Nitrification des Ammoniaks und seiner Salze, II.
 - " 6. LUPKE: Ueber die Bedeutung des Kaliums in der Pflanze (Taf. XV).
 - "— MEYER: Untersuchungen über die Entwicklung einiger parasitischen Pilze bei saprophytischer Ernährung (Taf. XVI-XIX).
- Mittheilungen aus dem Naturwissenschaftlichen Verein für Neu-Vorpommern und Rügen in Greifswald. Jahrg. XIX (1887).
 - MÖLLER: Ueber das Verkommen der Gerbsäure und ihre Bedeutung für den Stoffwechsel in den Pflanzen.
- Mittheilungen, Botanische, aus den Tropen. Heft II.

SCHIMPER: Die epiphytische Vegetation Amerikas.

Mittheilungen der Geogr. Gesellschaft (für Thüringen) zu Jena. Bd. VII, Heft 1, 2.

HAUSSKNECHT: Beiträge zur Gattung Epilobium.

- Mittheilungen des botanischen Vereins für den Kreis Freiburg und das Land Baden.
 - No. 45. ZAHN: Sommer um den Feldberg.
 - ,, 46. LAGERHEIM: Mykologisches aus dem Schwarzwald.
 - " WINTER: Unsere Brunnenflora.

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- ,, KNEUCKER: Beiträge zur Flora von Karlsruhe.
- " Mez: Die amerikanischen Lauraceen des Döll'schen Herbars.

Nos. 49, 50.

- " Klein: Beiträge zur Technik mikroskopischer Dauerpräparate.
- " Neue Standorte aus der Pfälzer Flora.
- ,, KLEIN: Anton de Bary (Nachruf).

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- " Scheurle: Die badischen Weidenarten.
- ,, Schatz: Die badischen Ampferbastarde (continued in No. 53).

Mittheilungen des Vereins für Erdkunde. Halle a. S. 1888.

Schulz: Die floristische Litteratur für Nordthüringen, den Harz und den provinzialsächsischen wie anhaltischen Antheil an der norddeutschen Tiefebene.

- Mittheilungen, Monatliche, aus dem Gesammtgebiete der Naturwissenschaften (Huth). Bd. V.
 - No. 5. Huth: Nachricht von einer alten und wenig bekannten pharmazeutischen Flora,
 - " 6. Aschenson: Die Verbreitung von Achillea cartaliginea, Ledeb., und Polygonum danubiale, Kern. im Gebiete der Flora der Provinz Brandenburg.
 - " Höck: Einige Hauptergebnisse der Pflanzengeographie in den letzten 20 Jahren (continued in No. 7).
 - ,, 7. HAGER: Ueber die giftige Wirkung einiger Lathyrus-Arten.
 - " 8. HUTH: Die Verbreitung der Pflanzen durch die Excremente der Thiere.
 - ,, Höck: Phaenologisches aus Friedeberg, Nm.

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SEMLER: Die Veränderungen, welche der Mensch in der Flora Kaliforniens bewirkt hat.

Monatsschrift, Deutsche Botanische. 1888.

- No. 1. CALLMÉE: Beiträge zur Caricologie (continued in Nos. 4, 5).
- " Ludwig: Biologische Notizen.
- " Enrico: Neue Standorte einiger selteneren Rosen der italiänischen und südtirolischen Flora.
- " LORCH: Beiträge zur Flora der Laubmoose in der Umgegend von Mar-
- Nos. 2, 3. Schneider: Ueber Hauptspecies und Zwischenformen innerhalb der Piloselloiden.
 - ,, WIESBAUR: Verbreitung der Veronica agrestis in Oesterreich.
 - " Eine Naturforscherversammlung in Nürnberg (an unpublished paper by Schleiden).
 - " 4,5. Scheuerle: Ein südlicher Standort der Salix livida, Whlbg.
 - ", WETTSTEIN, VON: Zur Verbreitung der Veronica agrestis, L., in Niederösterreich.
 - ,, ARTZT: Zur Flora von Schluderbach in Südtirol (continued in Nos. 6, 7).
 - " WÖRLEIN: Neue und kritische Pflanzen der Umgegend von München.
 - " DÜRER: Der 'Hengster' bei Frankfurt a. M. mit seinen botanischen Schätzen.
 - .. GEISENHEYNER: Ueber eine Fasciation.
 - " König: Beitrag zur Algenflora von Cassel (continued in Nos. 6, 7).
 - "6, 7. FREYN: Beitrag zur Flora von Syrien und des cilicischen Taurus.
 - " KAULFUSS: Flora von Lichtenfels in Ober-Franken (continued in Nos. 8, 9).
 - "8, 9. SCHNEIDER: Uebersicht der sudetischen und systematische Gruppirung der europaeischen Archieracia (continued in Nos. 11, 12).
 - " WINTER: Pilatus.
 - " WIESBAUR: Zur Verbreitung der Veronica agrestis, L., in Ober-Oesterreich.
 - Beitrag zur Flora des Regnitzgebiets (zusammengestellt vom Bot. Verein in Nürnberg) (continued in Nos. 11, 12).
 - " RÖLL: Die Thüringer Laubmoose und ihre geographische Verbreitung.
 - " 10. SAGORSKI: Plantae criticae Thuringiae.
 - ,, ZIGERT: Carex paniculata × canescens, n, hybr., C. silesiaca, m. ein neuer Carex-bastard in Schlesien.
 - " CALLIER: Botanische Excursion ins Riesengebirge.

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" - Knuth: Die Orobanchen Schleswig-Holsteins.

" II, I2.

GEISENHEYNER: Bemerkungen und Zusätze zur dritten Auflage der Excursionsflora des Grossherzogtums Hessen von Dosch und Scriba.

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HUTH: Die Hakenklimmer (mit 2 Taf. und 6 Holzschn.); Ueber stammfrüchtige Pflanzen.

Schriften der physikalisch-ökonomischen Gesellschaft zu Königsberg i. Pr. XXVIII.

ABHANDLUNGEN.

CASPARY: Einige neue fossile Hölzer Preussens nebst kritischen Bemerkungen über die Anatomie des Holzes und die Bezeichnung fossiler Hölzer.

ABROMEIT: Gedächtnissrede auf Prof. Dr. Robert Caspary.

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SITZUNGSBERICHTE.

KLIEN: Ueber die Funktionen der sogenannten Leguminosenknöllchen.

: Ueber das Wurzelwachsthum entlaubter Bänme.

CASPARY: Ueber neue fossile Hölzer aus Ost- und West Preussen.

RITTHAUSEN: Ueber die Alkaloïde der Lupinen.

KLIEN: Ueber vegetative Bastarderzeugung durch Impfung.

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HARTIG: Ueber den Einfluss der Verdunstungsgrösse auf den anatomischen Bau des Holzes.

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MAGNUS: Einige Beobachtungen betreffend die Bestäubung von Spergularia salina, Presl.

-----: Ueber das epidemische Auftreten einer Urophlyctis-Art, die er U. Kriegeriana nennt, auf Carum Carvi.

WITTMACK: Mittheilung des Herrn A. Ernst in Caracas über fischvergiftende Pflanzen.

------: Ueber Sanseviera longiflora, Sims.

----: Ueber den Blütenstand einer für den Gartenbau neuen Bromeliacee.

SCHRODT: Ueber eine Vergiftung durch Colchicum autumnale.

MAGNUS: Ueber Wurzeln von Passiflora mit kleinen seitlichen Verdickungen verursacht von Heterodora.

SCHARRER: Ueber Volksarzneimittel in Transkaukasien.

MAGNUS: Ueber eine epidemische Erkrankung der Gartennelken.

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KOSMAHL: Die Fichtennadelröthe in den Sächsischen Staatsforsten.

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TAMBA: Die Herkunft der Zellkerne in den Gefässthyllen von Cucurbita. (Abb. 88).

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MAGNUS UND KÖHNE: Bericht über die 46. Hauptversammlung zu Buckow am 5. Juni 1887.

MAGNUS: Ueber den Einfluss des Standorts auf die Ausbildung des Leontopodium alpinum, Cass.; Auftreten von Laubblättern unter den Kätzchen von Populus tremula; Ueber die Bestäubungsverhältuisse von Silene inflata, Sm. in den Alpen bei Zermatt; Ueber die Verbreitung von Caeoma Chelidonii, Magn.; Berichtigung; Verzeichniss der am I. Mai, 5. und 6. Juni bei Buckow gesammelten Pilze.

WITTMACK: Ulex europaeus, L. und Zelkova acuminata.

SCHEPPIG: Cytisus Adami, hort. ohne Rückschläge.

ASCHERSON: Reisebriefe aus Aegypten.

: Bericht über die 47. Hauptversammlung zu Berlin am 29. Oktober 1887.

MEZ: Myrmekophilie der Lauracen-Gattung Plemothyrium.

THOMAS: Ueber das durch eine Tenthredinide erzeugte Myelocecidium von Lonicera.

----: Bemerkungen über die Holzkröpfe von Birken, Aspen und Weiden.

MAGNUS: August Wilhelm Eichler. Nachruf (mit Bildniss).

KARNBACH: Die bisher im Königlichen Botanischen Garten zu Berlin beobachteten Uredineen und Ustilagineen mit Einschluss von Protomyces. Mit Vorwort von P. Magnus.

MAGNUS: Nachtrag hierzu.

-: Peronospora effusa, Grev. auf den überwinterten Spinatpflänzchen bei Berlin, nebst Beobachtungen über das Ueberwintern einiger Peronospora-Arten.

LUDWIG: Die Farnpflanzen des reussischen Vogtlandes.

SEEMEN, VON: Carex acutiformis × filiformis, Aschs.; Melica picta, C. Koch, bei Sulza in Thüringen.

Beyer: Ueber Primeln aus der Section Euprimula, Schott (Primula veris, L.) und deren Bastarde.

MEZ: Beiträge zur Kenntniss des Umbelliferen-Embryos.

WINKLER: Die Keimpflanzen der Koch'schen Clematis-Arten.

-: Die Keimpflanze von Corylus Avellana, L. (Taf. I).

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Schinz: Beiträge zur Kenntniss der Flora von Deutsch-Südwest-Afrika und der angrenzenden Gebiete, I.

LAUX: Ein Beitrag zur Kenntniss der Leitbündel im Rhizom monokotyler Pflanzen (Taf. II. und III. und 1 Holzschnitt).

WINKLER: Ueber das Artenrecht des Chenopodium opulifolium, Schrad. und C. ficifolium, Sm. (mit 3 Holzschn.).

POTONIÉ: Ueber die fossile Pflanzengattung Tylodendron.

FRIEDEL: Die alten Weiden von Berlin.

ASCHERSON: Ueber Knuths Flora von Schleswig-Holstein.

VIRCHOW: Zwei Riesentannen in den Voralpen des Canton Bern.

SEEMEN, VON: Anemone ranunculoides × nemorosa bei Berlin gefunden.

MAGNUS: Peter Simon Pallas.

---: Robert Caspary. Nachruf (mit Bildniss).

-----: Ueber die Bestäubungsverhältnisse der Spergularia salina, Presl, nebst einer brieflichen Mittheilung von Aug. Schulz.

JACOBASCH: Mittheilungen: A. Teratologisches (Cyclamen persieum, Gagea pratensis, mit Holzschn., Papaver somniferum und Dipsacus silvester); B. Abnorme Blüthenzeit von Papaver Rhoeas; C. Floristisches.

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GURTT: Ueber die verkieselten Coniferenstämme in Apache County.

BRANDIS: Ueber die Bambusen von Birma.

KÖRNICKE: Ueber die wilde Stammform des Duhu, Pennisteum spicatum, Körn.

Kreusler: Ueber Assimilation und Athmung der Pflanzen.

Versuchsstationen, Die Landwirthschaftlichen (Nobbe). Bd. XXXV.

Heft 3. NOBBE, SCHMIDT, HITTNER UND RICHTER: Ueber den Einfluss der Keimungsenergie des Samens auf die Entwicklung der Pfianze.

den Einfluss der Kreuzbefruchtung auf die Nachkommenschaft.

" - HEINE: Die physiologische Bedeutung der sogenannten Stärkescheide.

" 4. DIETRICH: Zur Kenntniss des indischen Weizens.

Heft 5, 6. MAYER: Heilung der Mosaikkrankheit des Tabaks.

" -- PLANTA, VON: Ueber die Zusammensetzung der Knollen von Stachys tuberifera.

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Bd. XX, Heft 4.

BISCHOFF: Ueber getrocknete Pilze des Handels.

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KOLBE: Zur Kenntniss von Insektenbohrgängen in fossilen Hölzern (Taf. XI),

Zeitschrift des deutschen Palästina-Vereins.

Bd. XI, Heft 2.

ANDERLIND: Die Fruchtbäume in Syrien, insbesondere Palaestina.

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" 2. HORN: Ueber das Oel der Samen von Jatropha Curcas.

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Heft I SALKOWSKI: Ueber das eiweisslösende Ferment der Fäulnissbacterien und seine Einwirkung auf Fibrin.

Zeitschrift für Hygiene (Koch und Flügge).

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Neisser: Versuche über die Sporenbildung bei Xerosebacillen, Streptokokken und Choleraspirillen.

SMIRNOW: Ueber das Wesen der Abschwächung pathogener Bakterien (m. Tafel).

NUTTALL: Experimente über die bacterienfeindlichen Einflüsse des thierischen Körpers.

Bd. V, Heft I und 2.

ESMARCH: Die Milzbrandsporen als Testobjecte von Desinficientien.

CORNET: Ueber das Verhalten der Tuberkelbacillen im thierischen Organismus unter dem Einfluss entwicklungshemmender Stoffe.

KITASATO: Die Widerstandsfähigkeit der Cholerabacterien gegen das Eintrocknen und gegen die Hitze.

LÜDERITZ: Zur Kenntniss der anaëroben Bacterien (m. Taf.).

BABES: Ueber isolirt färbbare Antheile von Bacterien (m. Taf.).

CORNET: Die Verbreitung der Tuberkelbacillen ausserhalb des Körpers.

FRÄNKEL: Die Einwirkung der Kohlensäure auf die Lebensthätigkeit der Microorganismen.

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BAUMGARTEN: Zur Kritik der Metschnikoffschen Phagocytenlehre.

Zeitschrift für Naturwissenschaften (Halle).

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SCHLECHTENDAL, VON: Ueber Zoocecidien.

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AMTHOR: Ueber den Saccharomyces apiculatus.

Bd. XII, Heft 1-3.

JACOBSON: Ueber einige Pflanzenfette.

HOPPE-SEYLER: Ueber Huminsubstanzen, ihre Entstehung und ihre Eigenschaften. I. Ueber die Bildung von Huminsubstanzen in Pflanzen. II. Verhalten der Cellulose und des Holzgummi. III. Ueber die Zusammensetzung und Eigenschaften der Huminstoffe.

LIMBOURG: Ueber die antiseptische Wirkung der Gallensäuren.

POHL: Bemerkungen über künstlich hergestellte Eiweissnucleine.

Kossel: Ueber das Theophyllin, einen neuen Bestandtheil des Thees.

Zeitschrift für wissenschaftliche Mikroskopie (Behrens).

Bd. V. Heft 3.

GRIESBACH: Theoretisches über mikroskopische Färberei.

RESEGOTTI: Ulteriori esperienze sulla colorazione delle figure cariocinetiche.

HEINRICHER: Ist das Congoroth als Reagenz auf Cellulose brauchbar?

Zeitschrift, Jenaische, für Naturwissenschaft.

Bd. XXII (Neue Folge, Bd. XV), Heft 3 und 4.

STAHL: Pflanzen und Schnecken. Biologische Studie über die Schutzmittel der Pflanzen gegen Schneckenfrass.

BOVERI: Zellen-Studien (m. 15 Tafeln).

Zeitung, Botanische (Graf zu Solms-Laubach; J. Wortmann).

Jahrgang XLVI (concluded).

MÜLLER: Ueber die sogenannten Spermatien der Ascomyceten.

ZACHARIAS: Ueber Strasburger's Schrift, Kern- und Zelltheilung im Pflanzenreiche.

WORTMANN: Zur Beurtheilung der Krümmungserscheinungen der Pflanzen.

VÖCHTING: Ueber die Lichtstellung der Laubblätter.

KARSTEN: Ueber die Entwicklung der Schwimmblätter bei einigen Wasserpflanzen.

DE BARY: Species der Saprolegnieen (Taf. IX und X).

ENGELMANN: Die Purpurbacterien und ihre Beziehungen zum Licht. BEYERINCK: Die Bacterien der Papilionaceen-Knöllchen (Taf. XI). FISCHER: Zur Kenntniss der Pilzgattung Cyttaria (Taf. XII). HARTIG: Ueber die Bedeutung der Reservestoffe für den Baum.

GREAT BRITAIN.

Album, The Orchid.

Vol. VIII (July-Dec. 1888) contains plates and descriptions of—Houlletia Brocklehurstiana, Lindley; Vanda lamellata Boxalli, Rchb. f.; Dendrobium macrophyllum, A. Richard; Cypripedium Amesianum, Williams; Batemannia Colleyi, Lindley; Cattleya Laurenciana, Rchb. f.; Odontoglossum Rossii Amesianum; Masdevallia Harryana decora; Oncidium intermedium, Knowles and Westcott; Laclia purpurata Blenheimense, Hort.; Brassia Keiliana tristis, Rchb. f.; Odontoglossum vexillarium rossum, Hort.; Trichopilia tortilis, Lindley; Cypripedium Fitchianum, Hort.; Trichopilia tortilis, Lindley; Cypripedium Fitchianum, Hort.; Rodriguezia secunda, Kunth; Calasetum Bungerothii, N. E. Br.; Cattleya Gas Relliana alba; Calanthe masuca, Lindley; Odontoglossum engenes, Hort. Veitch; Disa racemosa, L.; Cattleya bicolor Measuresiana; Angraecum caudatum, Lindl.; Comparettia falcata, Poeppig et Endl.; Oncidium Jonesianum flavens, Rchb, f.

Annals and Magazine of Natural History. Ser. 6, Vol. II, Nos. 7-12.

KIDSTON: On the fructification of two coal-measure Ferns. (Pl. I.)

: On a new species of Calamite from the Middle Coal-measures (Eucalamites (Calamites) britannicus, Weiss Ms.). (Pl. VII.).

SCHNETZLER: Observations on a colouring-matter of the water of the Lake de Bret.

Annals of Botany.

Vol. II (continued).

No. VI. JOHNSON: Arceuthobium Oxycedri. (Pl. X A.)

RENDLE: On the development of the Aleurone-Grains in the Lupin. (Pl. X B.)

MURRAY AND BOODLE: On the structure of *Spongocladia*, Aresch. (*Spongodendron*, Zanard.) with an account of new forms. (Woodcuts 8-11.)

REID: Notes on the Geological History of the Recent Flora of Britain.

Hartog: Recent Researches on the Saprolegnieae, a Critical Abstract of Rothert's results.

MARSHALL WARD: Illustrations of the Structure and Life history of Puccinia Graminis. (Pl. XI, XII.)

VINES: On the systematic position of *Isoètes*, L. (second note).

RENDLE: On the occurrence of Starch in the Onion.

SCHÖNLAND: A modification of Pagan's Growing Slide. (Woodcuts 12 and 13.)

No. VII. CAMPBELL: The development of *Pilularia globulifera*, L. (Pl. XIII, XIV, XV.)

MURRAY AND BOODLE: A structural and systematic account of the genus Struvea. (Pl. XVI.)

SCHÖNLAND: Contributions to the Morphology of the Mistletoe (Viscum album, L.) (Pl. XVII.)

JOHNSON: On Sphaerococcus coronopifolius, Stachh. (Pl. XVIII.)

RIDLEY: On the foliar organs of a new species of *Utricularia* from St. Thomas, West Africa. (Pl. XIX.)

HARTOG: On the floral organogeny and anatomy of *Brownea* and *Saraca*. (Woodcuts 14-16.)

MARSHALL WARD: A lily disease. (Pl. XX-XXII.)

FARLOW: Apospory in Pteris aquilina. (Woodcuts 17-20.)

VINES: On the relation between the formation of tubercles on the roots of *Leguminosae* and the presence of Nitrogen in the soil.

FARMER: On the development of the endocarp in Sambucus nigra. (Woodcuts 21-23.)

Asclepiad, The. Vol. V. No. 18.

A history of original researches in Therapeutics. Atropa Mandragora.

Botanical Exchange Club of the British Isles. Report for 1887.

Bulletin of Miscellaneous Information. Royal Gardens, Kew, 1888.

No. 20. Colonial fruit (continued in Nos. 21, 22).

,, - India Rubber in Upper Burma.

,, 23. Lagos Rubber (Ficus Vogelii, Miq.).

,, - Liberian coffee at Straits Settlements.

,, - Tea oil and cake (Camellia Sasangua, Shb.).

,, - Demerara Pink Root (Spigelia anthelmia, L.).

" - Food Grains of India (Coix gigantea, Roxb.).

" - Toruba Indigo (Lonchocarpus cyanescens, Bth.).

" - Trinidad Ipecacuanha (Cephaëlis tomentosa, W.).

,, - Treatment of vines in France.

" - Huskless barley.

Bulletin of Miscellaneous Information (continued).

No. 23. Ramie (Boehmeria nivea, H. f.) (continued in No. 24).

,, 24. Inhambane Copal (Copaifera Gorskiana, Bth.).

" - Cultivation of Rice in Bengal.

,, - Silkworm Thorn (Cudrania triloba, Hance.).

" — Jamaica India Rubber (Forsteronia floribunda, Don.).

,, - Seedlings of sugar cane at Barbados.

Chronicle, The Gardeners'. Series 3. Vol. IV.

No. 80. ROLFE: Megaclinium scaberulum, n. sp.

,, - Vegetable products in Central Africa.

" — SMITH, W. G.: Disease of Garden Hellebores: Peronospora Ficariae, Tul. (Fig. 2).

" 81. REICHENBACH, F.: Thunia candidissima, n. sp.; Epidendron auriculigerum, n. sp.

" - Rolfe: Angraecum tridactylites, n. sp.

" - FOSTER: Iris Korolkowi (Fig. 3).

" — Pinus Sabiniana, Dougl. (Fig. 4).

,, - Westwood: The Pear Midge (Fig. 5).

,, 82. JOHNSON: Helichrysum devium, n. sp. (from Madeira).

,, - Ostrowskia magnifica, Regl. (Fig. 6).

" 83. REICHENBACH, F.: Megaclinium oxyodon, n. sp.; Aëranthus ophioplectron, n. sp.; Spathioglottis aurea, Lindl. (Fig. 9).

" — SMITH, W. G.: Disease of Ornithogalum. Puccinia Liliacearum, Duby (Fig. 11).

,, 84. Heuchera sanguinea (Fig. 13); Styrax obassia (Fig. 14).

,, 85. S.: Funkias (Fig. 17, F. grandiflora).

, - Homeria collina (Fig. 19).

,, 86. BAKER: Aloe (Eualoe) penduliflora, n. sp.

., - ROLFE: Masdevallia platyrachis, n. sp.

" — Cyclopodium Saintlegerianum (Fig. 20).

" - BAKER AND FOSTER: Irises.

,, - SMITH, W. G.: Disease of Lilies. Peronospora elliptica (Fig. 21).

" - NICHOLSON: Stuartia pseudo-Camellia, Max. (Fig. 22).

,, - A proliferous strawberry (Fig. 23).

" 87. REICHENBACH, F.: Saccolobium cerinum, n. sp.; Bollea hemixantha. n. sp.

" — Plagianthus Lyalli (Fig. 24).

,, - MUELLER, VON: The Melbourne Herbarium.

., - Schomburgkia tibicinis (Fig. 25).

" 88. REICHENBACH, F.: Odontoglossum Hrubyanum, n. sp.

, - Lithospermum graminifolium (Fig. 27); Lisianthus Russelianus (Fig. 28).

,, 89. DEWAR: Pentstemon rotundifolius, n. sp. (Fig. 31).

" - MASTERS: The Calabrian pine (Pinus pyrenaica, Lap. Fig. 32).

" - Arauja graveolens (Fig. 33).

" 90. REICHENBACH, F.: Phalaenopsis Buyssoniana, n. sp.

" - Rhododendron Colletianum, Aitch. et Hemsl. (Fig. 38); Convolvulus tenuissimus (Fig. 39).

" - Crocosma aurea (Figs. 40, 41).

" 91. ROLFE: Masdevallia punctata, n. sp.

Chronicle, The Gardeners' (continued). No. 91. W.: Chironia peduncularis (Fig. 42). ,, - Abnormal fruit of Opuntia (Fig. 43). " — Pentapera sicula (Fig. 45). ,, 92. REICHENBACH, F.: Oncidium robustissimum, n. sp. - MASTERS: Passiflora Miersii (Fig. 46). ,, - WOLLEY DOD: The gum Cistus. " - Ursinia pulchra (Fig. 47); Roupellia grata (Fig. 48). ,, - SMITH, W. G.: Black Canker of bulbs. " 93. Pterocarya fraxinifolia (Fig. 52). ,, - Juglans mandshurica (Fig. 53). " - Adventitious buds on Phalaenopsis Stuartiana (Fig. 54). ,, 94. Pseusdophoenix Sargenti: a new palm from Florida (Fig. 56). - Douglas: The genus Primula. " - Lilium nepalense (Fig. 57). " 95. Dragon trees in Madeira (illustrated). 96. Fraser: Enemies of the apple and pear (Figs. 59-67). - Rolfe: Catasetum fuliginosum, Lindl. " - Hippeastrum reticulatum (Fig. 68). ,, - DOUGLAS: The genus Stanhopea (Fig. 69). " 97. O'BRIEN, J.: Cypripedium Elliotianum, n. sp. ,, - ROLFE: The genus Polycynis. ,, - ELLACOMBE: Plant-names a thousand years ago. ,, - NICHOLSON: The Persimmon (Diospyros virginiana) at Kew (Figs. 71, 72); Caesalpinia japonica, Sieb. et Zucc. (Fig. 73). ,, 98. Rolfe: Dendrophylax Fawcetti, n. sp. " - Begonia boliviensis, Veitchii, socotrana (Figs. 75-77); Arthrotaxis selaginoides (Fig. 79). ,, 99. NEWBERRY: The early history of vine culture in England. - Crocosma aurea, var. maculata, Baker (Fig. 80). - Masters: Decaschistia ficifolia, n. sp. - Maxillaria fuscata (Fig. 81). " 100. Eucalyptus viminalis (Fig. 82). ,, - REICHENBACH, F.: Cynoches versicolor, n. sp. ,, - Calandrinia oppositifolia, S. Watson, sp. nov. (Fig. 83). ,, - Pinus Pinea (Figs. 84, 85). " 101. BAKER: Eucharis grandiflora, Planch., var. Moorei, Baker. ,, - Arundina bambusaefolia (Fig. 87). " - J. O. W.: Callidium (Gracilia) pygmaea (Fig. 92). " 102. BAKER: Lilium (Archelirion) Henryi, n. sp. ,, - Brown: Disa lacera, Sw. and var. multifida, N. E. Br. (Figs. 93, 94). ,, - NICHOLSON: Phillyrea decora (Fig. 96). ,, 103. Pinus Laricio (Fig. 97, 99). " - ROLFE: Catasetum Garnettianum, n. sp. " - REICHENBACH, F.: Cypripedium insigne, Wall., var. Horsmanianum, n. var. " - O'BRIEN: Satyrium carneum (Fig. 98).

"— Ficus Roxburghii, Wall. (with Plate). " 104. Arbutus Andrachne (Fig. 100). cxiv

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Chronicle, The Gardeners' (continued).

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" - Brown: Stapelia gigantea (Fig. 101).

" -- Crataegus mexicana, var. Carrierii (Fig. 104).

" — Coniocybe pallida (Fig. 105).

" 105. Symphyandra Hoffmanni, Pantozsek (Fig. 107).

" — J. O. W.: The red grub of the plum (Fig. 108).

" - Pinus Coulteri (Fig. 109).

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" 286. ARNOLD: Lathyrus tuberosus in Sussex.

" — BULMAN: The red leaf again: a reply (continued in No. 287).

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,, 160. Fungus Foray at Bramham and Harewood Parks.

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- " ARDISSONE: Le Alghe della Terra del Fuoco raccolte da Spegazzini.

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STARBÄCK: Kritisk utredning af Leptosphaeria modesta, Auct.

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FRIES: Terminologiska smånotiser.

GREVILLIUS: Om stammens Cygnad hos mågra lokalformer af Polygonum aviculare, L.

KJELLMANN: Skottets bygnad hos fam. Chordariaceae. LUNDSTRÖM: Några iakttagelser öfver Calypso borealis.

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KAURIN: Brachythecium Ryani, n. sp.

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ARRHENIUS: Stellaria ponojensis. HULT: En grupp af Salix alba.

Häftet 5.

FRIES: Några anmärkningar om Pilophorus.

----: Om Stenanthus curviflorus, Lönnr.

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JUEL: Morfologiska undersökningar öfver Koeningia islandica.

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KAALAAS: Nogle nye scandinaviske moser.

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